INTERSPECIFIC COMPETITION OF FALL ARMYWORM SPODOPTERA FRUGIPERDA (J.E. SMITH) PARASITOIDS, CHELONUS INSULARIS (CRESSON), COTESIA MARGINIVENTRIS (CRESSON) AND MICROPLITIS MANILAE ASHMEAD (HYMENOPTERA: BRACONIDAE)

By

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INTERSPECIFIC COMPETITION OF FALL ARMYWORM SPODOPTERA FRUGIPERDA (J.E. SMITH) PARASITOIDS, CHELONUS INSULARIS (CRESSON), COTESIA MARGINIVENTRIS (CRESSON) AND MICROPLITIS MANILAE ASHMEAD (HYMENOPTERA: BRACONIDAE)

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Interspecific competition within fall armyworm (FAW), Spodoptera Frugiperda (J.E. Smith), larvae by the larval parasitoids Cotesia (=Apanteles) marginiventris Cresson and Microplitis manilae Ashmead and the egg-larval parasitoid Chelonus insularis Cresson was studied. Experiments conducted with 4 larval age groups (1, 24-48h; 2, 49-72 h; 3, 73-96 h; 4, 97-130 h) of the fall armyworm revealed that the first 2 age groups were most suitable for the development of M. manilae. The developmental period of M. manilae ranged between 13-18 days. Highest parasitization was observed for M. manilae when 2 females were exposed to 20 hosts for 30 min at 26±1°C.

Cotesia marginiventris was a superior competitior relative to C. insularis and C. insularis was superior to M. manilae. Subsequent parasitization by either C. marginiventris or M. manilae or larvae exposed to C. insularis as eggs did not result in additive host mortality. Microplitis manilae females changed their behavior significantly by displaying a reduction of approximately 50% in host examinations, 45% in ovipositor probes, and 55% in apparent ovipositions when C. insularis parasitized larvae were presented. Cotesia marginiventris displayed a greater number on contacts, examinations and ovipositional attacks in larvae 3 and 6 days after initial parasitization by M. manilae.

The maximum reproductive potential for C. marginiventris was achieved in hosts 36 to 48 hours old and at a temperature of 25°C. The optimum parasitoid age for C. marginiventris during the host exposure period was 48 to 96 hours. Egg to adult developmental times at 25°C, were 17 and 26 days for C. marginiventris and C. insularis, respectively. In multiple parasitized larvae C. marginiventris appeared to physically attack and destroy the larvae of C. insularis. C. insularis was the predominant species that emerged from field cage but C. marginiventris was a better competitor at host densities above 120 eggs/larvae. The damage to upper leaves was significantly greater in non-parasitoid release plots than in parasitoid released plots.

INTRODUCTION

Chemical insect pest control has become a controversial management strategy for several reasons. Insect pests have frequently become resistant to pesticides, and the costs of developing and registering a new insecticide have risen sharply. There is also concern about the effects of pesticides upon human health and the environment. This combination of circumstances has prompted entomologists to seek alternative control strategies leading to the development of sophisticated techniques involving a wide array interdisciplinary approach that have been termed "integrated pest management". Along with the development of strategies such as breeding resistant plant varieties and the use of pheromones to disrupt communications, there has been a resurgence of interest in the use of entomophages.

Huffaker and Messenger (1976) defined biological control as the action of predators, parasites, and pathogens which maintains host densities at levels lower than would occur in the absence of these natural enemies. Despite the many successes obtained through the introduction and release of a pest's natural enemies, this classical biological control strategy has not always provided the desired degree of pest control. In this strategy of biological control, natural enemies are deliberately

imported to control introduced or native pests. General guidelines for locating, selecting and introducing agents for biological control have been discussed (Huffaker and Messenger 1976). Efforts should begin with a careful study of the life cycle of the target pest. If it appears that exotic competitors may be beneficial then foreign exploration should first begin in areas environmentally similar to the intended area of releases. Species that are candidates for introduction must be evaluated carefully to insure that they are indeed beneficial and that they themselves will not become pests.

Interspecific competition among natural enemies of a given host can be of a great importance in biological control. In classical biological control, the potential for interspecific competition exists when more than one species of natural enemy is released into the environment and utilizes the same host. Regarding such multiple species introductions, it has been suggested that such interpecific competition could possibly lead to a decline in the population regulation of the host (Watt 1965) although others have refuted this idea (Huffaker et al. 1971). In endemic host enemy associations, interspecific competition appears to play a crucial role in structuring the parasitoid guild (Force 1974) and probably influences the entire natural enemy complex as well. Generally, the outcome of the competition is physiologically determined

within the host. Thus, researchers may be unable to predict the outcome unless they can identify and duplicate the relevant elements of the pest's physiology under experimental conditions.

The parasitoid guild of Spodoptera frugiperda (J.E. Smith), the fall armyworm (FAW), provides a relevant host parasitoid association for assessing host and natural enemy relationships. The FAW is a sporadic and occasionally severe crop pest in the Southeastern United States where this species is known to be able to survive in winter (Luginbill 1928), though survival further north is thought possible only during exceptionally mild winters (Snow and Copeland 1969). In years of high population density, FAW larvae may cause over $300 million in damage (Mitchell 1979). Fifty three species of parasitoid species have been recovered from FAW larvae (Ashley 1979) and are responsible for significant reductions in FAW larval populations (Ashley et al. 1982). The principal parasitoids of the FAW either attack its eggs or the early instars and thus provide suitable models for the study of parasitoid interrelationships, especially with regard to interspecific competition between the egg-larval and larval parasitoids.

The following research was conceived to assess and investigate the competitive abilities between the parasitoid larvae of Chelonus insularis Cresson, Cotesia

(Apanteles) marginiventris Cresson, and Microplitis manilae Ashmead. The objectives of the study were to (1) study the biology of M. manilae an imported larval parasitoid of Spodoptera spp in Thailand, (2) investigate interspecific competition between larvae of the parasitoids C. insularis, C. marginiventris, and M. manilae, (3) examine the effects of host and parasitoid age, and temperature on the outcome of interspecific competition, and (4) study the functional response of C. marginiventris when exposed to different densities of FAW larvae previously parasitized by C. insularis.

LITERATURE REVIEW

The Fall Armyworm, Spodoptera frugiperda (J.E. Smith)

The fall armyworm (FAW), Spodoptera frugiperda (J. E. Smith), (Lepidoptera:Noctuidae) inflicts damage on a large number of agricultural crops, especially those belonging to the family Graminae, in the Southeastern and Central United States (Luginbill 1928) and Central America (Andrews 1980). Corn (Zea mays L.), Sorghum (Sorghum bicolor (L.) Moench) and Bermudagrass (Cynodon dactylon (L) Pers.) are the favored agricultural hosts for the FAW (Sparks 1979). Economic damage to other crops, including alfalfa, peanuts, rice and soybean, has also been documented (Navas 1974, Morrill 1973, Pitre 1979). Tietz (1972) lists 68 genera of plants, many of which are weed species, that are attacked by the FAW.

Seasonal Distribution

Unlike most other insects in the temperate region, the FAW has no mechanism for diapause. Thus, the species overwinters commonly in South Florida and Texas, where temperatures do not destroy it and where hosts are continually available (Luginbill 1928). In mild winters it is also found in Louisiana and Arizona (Snow and Copeland 1969). During the spring and summer the FAW

disperses again throughout the eastern and central United States, and, in some years, into Southern Canada (Luginbill 1928). This migration is assisted by weather fronts (Sparks 1979). Several hypotheses have been advanced to explain the seasonal distribution of damaging populations of FAW (Rabb and Stinner 1978; Walker 1980; Barfield et al. 1980). Walker (1980) presented 3 models to account for seasonal distribution patterns. Diffusion and freeze-back and return flight (Walker 1980), "pied piper" effect similar to diffusion and freeze back (Rabb and Stinner 1978) and a model on seasonal distribution patterns as combinations of short and long range movements, as well as periodic overwintering in as yet undiscovered habitats (Barfield et al. 1980) explained this aspect.

Life History

The life cycle of the FAW has been described by Luginbill (1928), Vickery (1929), Sparks (1979) and Keller (1980). The adults are nocturnal and at dusk initiate flying near host plants that are suitable for feeding, oviposition, and mating. Mitchell et al. (1974) showed that peak activity of adults occurred 6 hrs after sunset and another small peak occurred approximately 3 hrs later. Oviposition may occur on host plants where as many as

several hundred eggs may be laid in a mass and covered with scales. Total oviposition by a female may exceed 2000 eggs over a period of up to 23 days (Luginbill 1928). As larvae hatch from the eggs, they eat their egg shells (Morrill and Green 1973), and as a result of negative phototactic and geotactic behaviors, the first instars move into the whorls of corn and sorghum (Pitre 1979). The larvae feed preferentially on the developing leaves and at high densities will eat the mature leaves, tassels, ears, and the inner portions of the stalk (Luginbill 1928, Morrill and Green 1973). Development proceeds through 6, sometimes 7, and rarely 8 instars (Keller 1980). Temperature, larval nutrition, and probably egg nutrition were factors affecting instar number in FAW (Keller 1980). Mature larvae drop to the ground and pupate in the soil within a chamber located 2 to 8 cm below the surface (Luginbill 1928). Pupation depends upon soil texture, moisture, and temperature (Sparks 1979). Pupae have been found on plant parts during severe outbreaks (Burkhardt 1953). After eclosion, the adults find their way to the soil surface, locate a plant or other object on which to cling, and inflate their wings (Sparks 1979). There is also evidence that different host plants (Roberts 1965, Pencoe and Martin 1981) and different temperatures affect the biology of FAW (Barfield et al. 1978).

Roberts (1965) reported that the larval diet can affect the duration of larval period, pupal size, adult longevity, fecundity, and egg viability.

Economic Status

In some years FAW larval densities are low and not economically important while in other years high densities inflict serious economic losses (Sparks 1979). The FAW was recorded as an injurious pest in Georgia in 1797, and in Florida in 1856 (Sparks 1979).

Damaging populations of FAW appear to occur irregularly (Barfield et al. 1980). FAW infestation levels are unpredictable (Barfield et al. 1980) and conditions conductive to outbreaks are not well understood (Keller 1980).

The FAW causes damage to corn by feeding on the developing leaves within the whorl. In areas with severe infestations the tassels, ears, mature leaves and stalks are also consumed (Painter 1955). Defoliation ranges from skeletonization of leaves by early larval instars to complete leaf consumption by large larvae. Annual losses due to larval feeding are estimated to be between $300 to 500 million in the United States (Mitchell 1979). Larval food consumption has been studied by Luginbill (1928) and Barfield et al. (1980).

Natural Mortality

Various abiotic and biotic agents act as mortality agents of FAW populations in the field. Physical environment and natural mortality factors may act singly or in combination to determine the annual distribution pattern and densities of FAW populations (Barfield et al. 1980). Among abiotic environmental factors, temperature appears to be an important limiting factor (Barfield et al. 1980). Low temperature may be the most important factor limiting the winter survival of FAW (Luginbill 1928, Wood et al. 1979). Andrews (1980) reported that torrential daily rains for several days result in drowning of small larvae or washing them out of the whorls in corn in Central America.

Cannibalism among larvae is an important factor limiting population densities (Luginbill 1928). Mortality attributable to cannibalism and intraspecific competition is positively correlated with larval density (Wiseman and McMillian 1969). Olive (1955) reported that first instar larvae may destroy adjacent unhatched eggs while in the process of devouring their own egg shells. Ashley (Pers. Comm. 1985) studied the factors influencing cannibalism in FAW and showed that the larval density in combination with the amount of eatable surfae area affected cannibalism more significantly than did the amount of non-eatable surface area, diet volume, or photoperiod.

Natural mortality inflicted on FAW larvae by natural enemies (parasitoids, predators and pathogens) in both agricultural and wild host plant communities is believed to play a substantial role in density regulation (Barfield et al. 1980). Ashley (1979) presented detailed information about the classification and distribution of the FAW parasitoids and noted that 53 species from 43 genera and 10 families have been reared from FAW larvae. Among them 18 species occur in North America; 21 species occur in Central and South America; and 14 species are common to all three regions (Ashley 1979). Parasitoid species attacking FAW vary between different agroecosystems. For example, in a study by Ashley et al. (1980) in late planted field corn, 8 species of parasitoids, representing the families Braconidae, Ichneumonidae, Eulophidae and Tachinidae, were collected from FAW larvae feeding on corn and surrounding broadleaf signal grass. Chelonus texanus Cresson caused the highest mortality followed by Meterous autographae Musebeck and Euplectrus platyhypenae Howard. Nickle (1976) reported that 7 species caused parasitization of FAW larvae on peanuts and Apanteles marginiventris Cresson., M. autographae and Ophion spp were responsible for highest mortality. Ashley et al. (1983) in another study on parasitization of FAW larvae on volunteer corn, Bermudagrass (Cynondon dactylon (L)) and paragrass

(Brachiarie mutica (L)) reported that C. insularis Cresson was the principal parasitoid on corn and C. insularis and A. marginiventris were the major parasitoids on Bermudagrass while M. autographae parasitized the highest proportion of hosts in paragrass, reflecting a host plant preference. The native parasitoids C. insularis and A. marginiventris were the primary species attacking FAW larvae in South Florida and they destroyed 63% of each of the first instars; M. autographae and Rogas laphygmae Viereck, as well as several tachinids and a group of unidentified ichnuemonids, accounted for the rest of FAW larval mortality (Ashley et al. 1982). Tingle et al. (1978) reported that parasitoid populations attacking the FAW on alternate host plants of, in or near crop fields may be important sources of parasitoids that subsequently attack FAW larvae in corn. Waddill et al. (1985) discussed the seasonal abundance of FAW parasitoids, C. insularis, Temelucha spp. R. laphygmae, and C. marginiventris in southern Florida. Mitchell et al. (1984) reported that FAW pheremone components had no significant effect on the level of FAW parasitization by C. insularis and Temelucha difficulis Basch. The successful rearing of a pupal parasite Diapetimorpha introita of FAW in the laboratory has also been documented (Pair et al. 1985).

Predators and pathogens are among other natural enemies found to play a less consistent role in regulation

of FAW populations. Agnello (1978) compiled a list of 10 species of Hymenoptera (8 vespids and 2 sphecids) and 6 Hemiptera (3 reduviids, 1 pentatomid, 1 nabid and 1 anthocorid), 12 Coleoptera (9 carabids, 2 cicindellids and 1 coccinellid) a mammal (skunk), 3 amphibians (2 Bufo spp and 1 Hyla spp) and a variety (13 species) of birds as predators of FAW. An earwig, Doru spp inhabits whorls of corn and sorghum and found to feed readily on small and medium sized FAW larvae (Andrews 1980).

The FAW is reported to be susceptible to at least 16 species of entomogenous pathogens which includes viruses, fungi, protozoa, nematodes and 2 strains of the bacterium Bacillus thuringiensis Berliner (Gardner and Fuxa 1980). Many of these occur naturally in FAW populations. A "poly hedrosis" presumably nuclear polyhedrosis virus (NPV) was reported as early as 1915 (Chapman and Glaser 1915) and a granulosis virus has also been identified from FAW larvae collected from sorghum (Steinhaus 1957). Fungi also are natural mortality factors in FAW populations. Three species have been reported and include Entomophthora sphaerosperma Fresenius (Charles 1941), Nomuraea rileyi (Farlow) Sampsom (Luginbill 1928) and Empusa spp (Luginbill 1928). The natural occurrence of a nematode Hexamermis spp in FAW larvae was reported from Venezuela (Gnagliumi 1962). The only protozoan reported to occur

naturally in FAW is Nosema laphygmae Weiser, a microsporidium from Colombia (Weiser 1959).

Management Strategies

The major management strategies reported to control FAW are insecticides (Young 1980), cultural control (Luginbill 1928) and host plant resistance (Wiseman et al. 1979). Young (1980) suggested the use of irrigation water as a carrier for insecticides, thereby supplying the volume of liquid needed to penetrate all of the plant sites, where FAW feed. Application of granular insecticides directly to the whorl has been a common practice in Central America (Andrews 1980).

The importance of mechanical and cultural control of FAW was first reported by Luginbill (1928). Black light traps and pheremone baited cylindrical electric grid traps have been used to monitor seasonal populations of FAW in Louisiana and Florida (Mitchell 1979). However, disposable sticky traps baited with pheromone (z)-9-dodecen-1-ol acetate have been used extensively in surveys in Georgia and Florida. These traps were found to be most effective in capturing FAW males when positioned approximately 1 m above ground and near around preferred hosts (Mitchell 1979).

Wisemann and Davis (1979) showed the importance of resistant plant varieties in managing FAW populations.

The resistance of corn variety "Antigua 2 D" to FAW has already been documented (Wiseman et al. 1973). Resistant varieties in sorghum, peanuts, Bermudagrass, rice, and millet have also been reported (Davis 1980).

Considering the important factors regulating FAW populations, action thresholds (AT) for grain sorghum have been developed (Martin et al. 1980). These action thresholds are estimated to be 10% of seedling sorghum possessing egg masses after flowering. However there is a lack of information in many areas which makes it difficult to derive dynamic AT and population models representing the dynamics and host interactions of the FAW.

The Larval Endoparasitoid Cotesia (=Apanteles) marginiventris Cresson

Origin and Distribution

Cotesia (=Apanteles) marginiventris is one of the most freqently recovered parasitoids from field collected FAW larvae. This parasitoid was originally described from Cuba, and is native to the West Indies (Muesebeck 1921). It has been previously classified as Microgaster marginiventris Cresson (1865), Apanteles grenadensis Ashmead (1900), A. laphygmae Ashmead (1901), Apanteles (Protapanteles) harnedi Viereck (1912) and most recently Cotesia marginiventris Cresson (Marsh 1978). It appears to have a wide distribution within the United States, especially in

the southern states viz. Arkansas, Florida, Georgia, Louisiana, Mississippi, Tennessee, North Carolina and South Carolina (Wilson 1933, Mueller and Kunnalacca 1979, Marsh 1978). Some 16 hosts of C. marginiventris have been reported (Miller 1977) and all are noctuids. No crop preference is shown by this parasitoid when attacking Trichoplusia ni (Hbn.) on various food plants in Mississippi (Boling and Pitre 1970).

Description

The egg and laral instars are described by Boling and Pitre (1970), and the adults by Muesebeck (1921). The egg is hymenepteriform, cylindrical with rounded ends. The caudal end is slightly curved, and has a short peduncle. The egg is 0.017 mm at the broad end, 0.088 mm in length at oviposition and the peduncle is 0.0005 mm long (Boling and Pitre 1970). The egg is found free in the hemocoel of the host larvae. Up to 7 eggs have been found in a single host when the host larva was exposed to several female parasitoids. However, superparasitization does not necessarily lead to multiple cocoon formation. Normally only 1 egg is found per host (Boling and Pitre 1970). The first instar larva is white and caudate and is usually found in the posterior part of the host's body. First instar larvae are never found attached to the host. The

larva has a caudal appendage which is a modification of the last abdominal segment into a fleshy organ and a caudal vesicle that increases in size with longevity. Allen and Smith (1958) reported some species of Apanteles as being cannibalistic in the first instar; but no cannibalism has been observed in C. marginiventris (Boling and Pitre 1970). The second instar is vesiculated with a prominent anal vesicle and the body becomes more robust. Allen and Smith (1958) suggested that the second instar may actually be two instars. The third instar is hymenopteriform with no anal vesicle. This larva tapers anteriorly and is creamy white at first, turning light brown upon emerging from the host (Boling and Pitre 1970). The molt to the third instar happens just prior to parasitoid emergence, which generally occurs at approximately the 4th abodminal segment in the dorsolateral area of the host. The parasitoid initially constructs a one sided crescent-shaped cocoon and after its body has become seated, the larva closes the open side of the cocoon. The cocoon is small (3mm long), ovoid, firm, smooth and composed of white silk surrounded by some looser threads. The pupa is exarate and enters pupation approximately 24 hrs after formation of cocoon. Adults can be identified using the keys of Marsh (1971) (to genus) and Muesebeck (1921) (to species). The black adult is about 2-5 mm long, has yellow legs and is recognizable by the

sculpturing on the abdomen and hind coxa, and the color and length of the hind tibial spurs (Marsh 1978).

Life Cycle

Cotesia marginiventris is an arrhenotokus larval endoparasitoid of several lepidopteran pests. Female parasitoids mate and oviposit within several minutes after emerging from the pupal case but are more aggressive when held for 24 hrs prior to host exposure (Boling and Pitre 1970). Mating occurs with the male approaching the female from the rear, tapping her with his antennae and then mounting on her for approximately half a second. Both sexes mate many times and freely with other individuals. Females often mate after having initiated egg laying (Boling and Pitre 1970).

The egg is laid in early instar hosts. According to Vickery (1929) first instars are parasitized before they disperse and Kunnalaca and Mueller (1979) reported that first instars are preferred. According to Boling and Pitre (1970), C. marginiventris perfers to oviposit in 2 day old larva of T. ni rather than in 1 day or 3 day old larvae of the same species. Later host instars are less preferred becase host larvae usually jerk violently and this movement interfers with oviposition (Kunnalaca and Mueller 1979). In general parasitization increases with

increased exposure time. Kunnalaca and Mueller (1979) reported that oviposition was accomplished quickly with a single ovipositor thrust and this occurred primarily during day light hours. Multiple oviposition was common especially when few hosts were offered to a parasite (Boling and Pitre 1970). Total fecundity ranged from 30 to 110 eggs per female (Kunnalaca and Mueller 1979).

Time required for the development of C. marginiventris from oviposition to cocoon formation ranged from 6 to 11 days at 30°C (Boling and Pitre 1970, Kunnalaca and Mueller 1979). Boling and Pitre (1970) reported the optimum time for development as 7 days in T. ni and Pseudoplasia includens (Walker) and 6 days in Heliothes virescens (F.) within 24 hours after existing host larva. Kunnalaca and Mueller (1979) reported an optimum developmental time of 8 days in Plathypena scabra (F). At 30°C and 25°C, development times from cocoon to adult ranged from 3-5 days and 4-7 days, respectively (Kunnalaca and Mueller 1979). The sex ratio (1.5:1) favored males at both 30°C and 25°C (Kunnalaca and Mueller 1979). Mean longevity of adults at 30°C and 25°C was 5.6±2.5 and 9.1±4.2 days, respectively and females lived longer than males at both temperatures (Kunnalaca and Mueller 1979).

Parasitization by C. marginiventris resulted in growth retardation of the host (Danks et al. 1979).

Ashley (1983) reported that parasitization of FAW larvae by C. marginiventris reduced maximum larval weights by 97%, compared to 6th instar nonparasitized larvae. C. marginiventris destroyed its host when the host reached the 4th instar. Hosts parasitized by C. marginiventris gained the least amount of weight, produced the least amount of frass, and had shortest life expectancies and the smallest head capsule widths compared to other parasitoids (Ashley 1983).

Loke et al. (1983) has described the behavioral sequence for host finding and oviposition for C. marginiventris on corn plants artifically damaged by 2nd instar larvae of the FAW and reported that highest parasitization rates occurred among 2nd instar larvae collected from leaf surfaces. Bioassay responses in C. marginiventris females to materials derived from FAW larvae were most intense for frass and somewhat less intense for larval and pupal cuticle materials, scales, exuviae and silk (Loke and Ashley 1984).

The Egg-larval Parasitoid Chelonus insularis Cresson

Origin and Distribution

Chelonus insularis Cresson is one of the key parasitoids regulating FAW populations in South Florida (Ashley et al. 1982). It has been previously classified

as C. texanus Cresson (1872), C. texanoides Viereck (1905), C. exogyrus Viereck (1905) and C. bipustulatus Viereck (1911) (Marsh 1978). C. insularis is distributed throughout in North, Central and, South America, and the West Indies and has been introduced into Hawaii and South Africa (Marsh 1978).

Description

The eggs of C. insularis are white, and cylindrical, and appear comma like in shape. They are slightly arcuate with both ends rounded, one being larger than the other (Glogoza 1980). The first instar larva has a prominent square head with easily distinguishable dark, pointed, mandibles and 7 body segments tapering from the thorax to the abdomen (Glogoza 1980). The larva floats in the host hemolymph. The second stage larva is cylindrical with a tapered head. The body of the third stage is also cylindrical and the head which is relatively narrow tapers in the front. C. insularis causes its host to burrow in the earth when the host reaches the 4th instar and to form a pupation cell. After completing this cell the parasitoid larva consumes the entire contents of the host and then pupates. The larva spins a cocoon by using a silky secretion and this cocoon is cylindrical with almost flat ends. Ashley (1983) found that of those FAW larvae

parasitized by C. insularis, 41% died in the 4th instar and 59% died in the 5th instar. An emerging adult tears the silky cocoon with its mandibles and escapes through the opening. The body length of the adult is 4.5-5.0 mm and description of adults is found in Marsh (1978).

Life Cycle

The female parasitoids can begin to lay eggs even if they have not mated. The antennae are used to locate the host, the female then lands on the eggs, positions herself, and then injects her eggs directly into the host egg. The female may lay continously for about an hour if left undisturbed. Superparasitism is common in the genus Chelonus (Broodryk 1969) and was observed in C. insularis when parasitizing H. virescens (F.) eggs (Ables and Vinson 1981). Ables and Vinson (1981) reported that C. insularis appeared to examine host eggs internally as well as externally and was able to detect previously parasitized hosts. The average time of development from oviposition to adult is about 26 days for males and 28 days for females. Rechav (1978) found similar results for other Chelonus spp. Greatest fecundity was obtained at 30°C (Glogoza 1980). Survival was highest at low temperatures and the greatest percentage of eggs was parasitized at 35°C (Glogoza 1980). Male biased sex ratios occurred at

20° and 40°C while at 35°C a 1:1 ratio was obtained (Glogoza 1980).

C. insularis can develop in many hosts. Besides S. frugiperda, it is also able to develop in Heliothes armigera (Hubner), Spodoptera exigua (Hbn), Ephestia sericaria (Scott) (Bianchi 1944). Marsh (1978) reported that hosts for North America include Ephestia elutella, (Hbn), Feltia subterranea (F), Heliothes zea (Boddie), Loxostege sticticalis, (L.) Peridroma saucia (Hbn), Spodoptera eridania (Ramer), Spodoptera ornithogalli (Guenee), Spodoptera praefica Grote, and T. ni.

Parasitization of FAW by C. insularis reduced host FAW larval weights by 70% and only 28% of the larvae parsitized by C. insularis lived past the 9th day and these larvae displayed an unusual increase in weight prior to destruction by the parasitoid (Ashley 1983).

Ashley et al. (1982) found that the native parasitoid C. insularis was the primary species attacking FAW in South Florida and it emerged from 71% of the parasitized larvae. C. insularis caused the highest mortality of FAW larvae collected from corn and broadleaf signalgrass (Ashley et al. 1980). Ashley et al. (1983) reported that C. insularis parasitized 44% of all FAW larvae collected from volunteer corn, Bermudagrass and paragrass and

regardless of the host plant, C. insularis had a parasitization rate 4 times greater than other competing parasitoids. Substantially higher percent parasitization was obtained for corn than on other hosts (Ashley et al. 1983). Ashley et al. (1982) reported that C. insularis parasitized the greatest proportion of FAW larvae having head capsule widths of 0.3 mm. Chelonus insularis was not recovered from larvae having head capsule widths greater than 1.8 mm. This very clearly showed that C. insularis is primarily an egg parasitoid with preference to early instars to lay eggs. Mitchell et al. (1984) reported that two FAW pheremone components (Z9DDA and Z9TDA) had no significant effect on the level of FAW parasitization by its principal parasite C. insularis. The sex ratio for C. insularis shifted from approximately 1:1 (Female:male) during spring to approximately 1:4 during the summer months but the reduced proportion of females during summer did not lower parasitization levels by C. insularis.

The Larval Endoparasitoid Microplitis manilae

Description and Distribution

Microplitis manilae (Ashm) is reported as an important larval parasitoid of Spodoptera spp in Thailand (Shepard, Pers. Comm 1982). This parasitoid is not

indigenous to the United States, and was imported from Thailand through the USDA, Stoneville Research Quarantine Facility, Mississippi.

No taxonomic or distribution literature was located for M. manilae. The length of antennae in males is longer than for the female. However, Marsh (1978) described a closely related spp M. melianae Viereck. An unsuccessful attempt was made to establish M. manilae in the FAW overwintering range in South Florida (Ashley, Pers. Comm. 1983).

The adults are ready to oviposit soon after emergence. They will oviposit in FAW larvae for a period of 16-17 days. Different species of Microplitis attack the early larval instars of their hosts (Altahtawy et al. 1976). The female deposits an egg through the integumant of host larva into the hemolymph. The egg is elongated, oval and translucent white in color. The first instar is caudate with a relatively large head and the second instar is vesiculate and creamy white. After the parasitoid larva molts into the third instar, it emerges from the host (FAW) and spins a cocoon. Although the host remains alive after the parasitoid emerges, the host does not develop further and stops feeding. The parasitoid larva exits the host and pupates outside. A single parasitoid normally develops from each host even after

superparasitism. However, development of two parasitoids per host occurred more frequently when larger hosts were provided. Biology of M. demolitor imported from Queesland, Australia has been described by Shepard et al. (1983).

Interspecific Competition

By definition competition occurs when two or more organisms interfere with or inhibit one another (Pianka 1970). Smith (1929) defined "multiple parasitism" to designate the type of parasitization in which the same individual host insect is inhabited simultaneously by the young of two or more different species of primary parasitoids. Fisher (1961) reported that this type of multiparasitism resulted in competition between the parasitoids. The occurrence of this type of multiparasitism depends primarily upon the oviposition behavior of the two parasitoids in response to hosts that are already parasitized. In general, parasitoids require a host organism for egg deposition and the development of immature stages. Typically, the progeny of one or neither parasitoid will survive when individuals of different species parasitize a single host organism (Salt 1961). Therefore interspecific competition between parasitoids for hosts may be a vital component influencing guild composition (Zwolfer 1970). Interspecific competition among parasitiods may even

result in the competitive exclusion of certain species (Debach and Sundby 1963).

In many cases of interspecific competition, one species has an intrinsic superiority over its opponent and invariably destroys it, by the use of its mandibles (Pemberton and Willard 1918, Simmonds 1953) or by an unspecified means of physiological suppresion (Muesebeck 1918, Fisher 1961, Salt 1961).

More commonly there is no intrinsic superiority on the part of either parasitoid, and free competition occurs between them, the victor completing its development and the loser dying, either as an egg or a young larva. Several suggestions have been made in the literature as to the possible mechanism of competition between such solitary endoparasitic species. In the first place, the older parasitoid is presumed to survive by eliminating the younger through starvation (Fiske and Thompson 1909) thus emphasizing the importance of time of oviposition as the determining factor in competition. Secondly, cases of direct physical attack by one parasitoid on another using the mandibles for fighting has been recorded (Simmonds 1953). In these cases neither competitor has an intrinsic advantage over the other and the result of competition is apparently decided by the time of oviposition. The third suggestion is that one parasitoid eliminated the other by physiological suppression, either by conditioning the hemolymph of the host so that it becomes unsuitable for

the development of any successor (Van den Bosch and Haramoto 1953, Johnson 1959) or by the postulated secretion of a toxic substance which kills the opponent (Thompson and Parker 1930).

Competitive exclusion by previously introduced parasitoids has been viewed as one of the factors that explains the failure of introduced natural enemies in classical biological control to become established (Ehler and Hall 1982). The competitive exclusion hypothesis has been subject of considerable debate in the literature. Turnbull (1967) favored the competitive exclusion hypothesis while Van den Bosch (1968) rejected it. However, Ehler and Hall (1982) presented empirical evidence in support of competitive exclusion and stated that this could possibly lead to the extinction of an effective natural enemy. In fact, Force (1974) showed that a very effective natural enemy may in fact be an inferior competitior. Thus Ehler and Hall (1982) suggested that (1) simultaneous release of several species of natural enemies should be avoided due to interspecific competition between them that may lead to a lower establishment rate and (2) extra care should be taken in establishing species where incumbent species of natural enemies exist. However Moon (1980) reported that while the principle of competitive exclusion may be simple and attractive, it may not adequately apply to the heterogenous real world.

In classical biological control, the potential for interspecific competition exists when more than one species of natural enemy is released into the environment. Regarding such multiple species introduction, it has been suggested that such interspecific competition could possibly lead to a decline in population regulation of the host (Turnbull and Chant 1961, Watt 1965) although others have refuted this as a general phenomenon (Huffaker et al. 1971). Empirical evidence generally supports multiple species introductions (Ehler 1978). However, such evidence comes largely from successes involving multiple species releases without regard to instances where such releases did not yield total success (Ehler 1977). Miller (1977) suggested the possiblity that intrinsically superior competitors which exhibit a relatively low reproductive capacity would displace or interfere with intrinsically inferior competitors which exhibit a relatively high reproductive capacity. There is a concern that such competition would result in decreased parasitization rates. A computer simulation by Watt (1965) and a greenhouse study by Force (1970) suggested that such a reduction in the proportion of parasitization is possible.

Other things being equal, intrinsically superior species imported in biological control programs probably become established more easily than intrinsically inferior

ones. Examples of intrinsically superior parasitoids that have achieved such a role are two braconids, Opiun oophilus Full. (Bess and Haramoto 1958) and Macrocentrus ancylivorus Rohw. (Boyce and Dustan 1958). On the other hand, an intrinsically inferior species may achieve a higher level of parasitization in the field than its rivals if it is extrinsically superior to them. For example, Spalangia cameroni Perk., an intrinsically inferior species, parasitized more house fly pupae than all other species combined because the females were able to penetrate more deeply into areas containing hosts (Mourier and Hannine 1969). Obviously, an intrinsic superiority of one parasitoid over another may result in the waste of some parasitoids, but this effect, as pointed out by Smith (1929), is likely to be an insignificant factor in the comparative field efficiencies of two competing forms.

Case Studies

The superiority of Metaphycus inteolus (Timberlake) over Microterys flavus Howard inside the host (Coccus hesperidium) in the field was contrary to the pattern of dominance of both species when they competed within the host (Bartlett and Ball 1964). Arther et al. (1964) showed interactions between a braconid, Orgilus obscurator (Nees), and an ischneumonid, Temelucha interruptor, inside

the pine shoot moth, Rhyaciona buoliana Schiff. They reported that T. interruptor attacked more host larvae that had been previously parasitized by O. obscurator than unparasitized hosts. Vinson (1972) reported that in interspecific competition between larval parasitoids Cardiochiles nigriceps Viereck and Campoletis perdistinctus (Viereck) on tobacco budworm, H. virescens, that C. perdistinctus had a slight advantage over C. nigriceps when oviposition by the 2 species occurred at about the same time. Part of the reason for the advantage by C. perdistinctus may be more rapid growth rate of its larvae and a shorter egg development period. When the competitors were of similar age, one was eliminated through physical combat. When one competitor is 1 or 2 days older it was able to destroy several eggs of the younger competitor. However when older parasitoid is 4 days old the younger larvae is eliminated through physiological suppression (Vinson et al. 1972). Such suppressed larvae failed to grow and were inactive although they may be alive. When one of the tobacco budworm parasitoids was old or it eliminated the younger competitor by physiological suppression (Vinson 1972). Fisher (1961) also presented evidence of physiological suppression of younger larvae by the older competitor through the reduction of oxygen available to the younger larva. Wylie (1972) reported that only one parasitoid

species survived in interspecific competition among the pupal parasitoids Nasonia vitripennis (Walk)., Muscidifura zaraptor K. & L. and Splangia cameroni Perk. Nasonia vitripennis and M. zaraptor were both intrinsically superior to S. cameroni if the attacks on the hosts by their females preceded, were simultaneous with, or followed by up to 48 hrs those by females of S. cameroni. Nasonia vitripennis was intrinsically superior to M. zaraptor if its attacked preceded that by M. zaraptor by at least 24 hrs. The success of N. vitripennis when competing with S. cameroni was due to differences in rates of egg and larval development and of host utilization by the two species. In a similar study by Wallner et al. (1982), larval parasitoids Apanteles melanoscelus Ratzburg. and Rogas lymantriae (L.) inside the host Lymantria dispar (L.) both attacked the previously parasitized larvae but the parasitoid attacking the host first was more successful.

The studies on multiparasitism between the internal larval parasitoids of Rhyacionia buoliana Schiff. revealed that interspecific competition took place between the first instar larvae through direct physical attack (Schroder 1974). However there are instances where these internal parasitoids have coexisted within the host larva and this provides a good example of a system of

"counter-balanced competition" (Zwolfer 1970). In such systems, the competitive inferiority of a parasitoid species in multiple parasitism is compensated for by a superiority in other attributes such as searching efficiency and synchronization with the host's life cycle (Schroder 1974).

Weseloh (1983) reported that neither of the parasitoids A. melanoscelus nor Compsilura concinnata (Meigan) destroyed each other inside the host Lymantria dispar and both emerged from about 11% of the hosts. These results showed that both parasitoids appeared to be remarkably tolerant of each other in the same host and this probably happened because they fill different niches and so do not compete with each other within the host.

The larval parasitoids Campoletis sonorensis (Carlson) and Microplitis croceipes Cresson are intrinsically superior to C. insularis and physically attacked the latter inside the host, H. virescens (Vinson and Iwantsch 1980). In a similar study, Miller (1977) reported that C. insularis larvae competing with A. marginiventris inside Spodoptera praefica (Brote) were dwarfed and nearly killed due to competition. A second experiment involving C. insularis and Hyposoter exigue (Vierek) yielded a similar result where H. exigue was a superior intrinsic competitor relative to C. insularis and C. marginiventris.

In a study on impact of native parasitoids on FAW in Southern Florida, Ashley et al. (1982) described a mirror image pattern of parasitization between C. insularis and Temelucha spp collected from the FAW larvae. This increase-decrease and decrease-increase pattern between these two parasitoids may be indicative of interspecific competition between these parasitoids (Ashley et al. 1982). Mitchell et al. (1984) reported the effect of two FAW pheremone components (Z9DDA and Z9TDA) upon population dynamics of its larval parasites and found that C. insularis was the predominant species followed by T. difficilis whose parasitization rate of FAW larvae was initially high and then remained relatively constant for the remainder of the experimental period. The explanation for this type of parasitization pattern was that C. insularis was a better internal competitor than T. difficilis (Mitchell et al. 1984).

BIOLOGY AND HOST ACCEPTANCE OF MICROPLITIS MANILAE (HYMENOPTERA:BRACONIDAE) REARED ON FALL ARMYWORM LARVAE

Introduction

The fall armyworm (FAW), Spodoptera frugiperda (J.E. Smith), is a major pest of corn and Bermudagrass in the southeastern United States (Luginbill 1928) and may extend its range as far north as the Canadian border during the summer and fall months (Snow and Copeland 1969). However, since this pest has no mechanism for diapause or overwintering its populations are restricted to portions of south Florida and Texas during the winter months (Luginbill 1928). Average estimates of annual crop losses caused by the FAW exceed $300 million (Mitchell 1979). Therefore, reducing the density of overwintering FAW populations may result in a significant decrease in the amount of damage done by this pest.

Microplitis manilae (Ashmead) is a parasitoid of Spodoptera spp. in Thailand from where it was imported into the United States. Even though the FAW does not occur in Thailand, M. manilae develops successfully in larvae of the FAW under laboratory conditions (Shepard, personal comm. 1982). The biologies and distributions of

some members of this genus are known (Hafez 1951, Putter and Thewke 1970). Lewis (1970) describes the life history of M. croceipes (Cresson) for Heliothis spp. and reports that the parasitoid prefers 1st and 2nd instars as hosts. No research dats could be found that document the life cycle and host age acceptance of M. manilae developing within FAW larvae, nor has this parasitoid been reported as a natural enemy of FAW anywhere within its range (Ashley 1979).

The objectives of our research are to gain relevant information about the biology and host age acceptance of M. manilae when reared on FAW larvae. This information may prove useful in mass production of this parasitoid for inoculative or perhaps inundative releases should M. manilae eventually demonstrate the potential of becoming a significant mortality agent of FAW populations.

Materials and Methods

Female parasitoids were 24 hrs old and has been exposed to males since female eclosion. Each replicate consisted of exposing FAW larvae (number varied according to experiment) to 6 female parasitoids in a plastic container (7 x 10 cm diam) with 2 screened vents (1.5 x 3.0 cm) and having honey streaked on the underside of the

lid. During host exposure, FAW larvae fed on cubes (3 cm^3) of pinto bean diet (Leppa et al. 1979) after which the larvae were transferred individually to 30-ml plastic cups that contained pinto bean diet where they remained until their fate was determined. FAW larvae were kept as 23±2°C, 70±2% RH and under a 14:10 LD photoperiod. These larvae were divided into 4 groups depending on their age: 1, 24-48 hrs; 2, 49-72 hrs, 3, 73-96 hrs; and 4, 97-130 hrs. Hosts older than 130 hrs were excluded because M. manilae females would not accept them as hosts. The laboratory rearing method for M. manilae consisted of exposing parasitoids to approximately 50 FAW larvae which were 48-72 hrs old for 3-5 hrs.

Age group acceptance--Depending on host availability 4-6 replicates of 3-4 FAW larvae of the same age group were presented to two female M. manilae for 30 min. on the same day. Data from 4 consecutive days comprosed a single test and tests were replicated 4 different times.

Developmental rates--Microplitis manilae were exposed for 24 hrs to hosts in the four age groups. Parasitoid developmental times were determined from oviposition to pupation and from pupation to adult emergence. Progeny sex ratios were recorded for each age group.

Adult longevity--Freshly eclosed parasitoids were exposed to hosts under continuous light at 26±1°C and longevity was recorded for 2 groups: (1) the females (n=41) and males (n-57) were separated into different cages and (2) both sexes were kept together and allowed to mate for 2 hrs and then to oviposit for 24 hrs inside a plastic container with 20 FAW larvae. After the host exposure period, larvae were removed and adult parasitoids were retained in the plastic containers.

Time of host exposure--In order to determine optimal host exposure time, 2 female M. manilae were exposed to 20 hosts from the 2nd age group for 15, 30, 45 and 60 min. and then removed. Four replicates were run.

Results and Discussion

Parasitoids displayed the highest host acceptance for 1st and 2nd age group larvae and a lesser acceptance for 3rd age group larvae (Table 1). Highest parasitization rates occurred most frequently in 2nd age group larvae. Significantly fewer 4th age group larvae were parasitized compared to larvae of other groups, and there were several occurrences of significant differences in host acceptance between 2nd and 3rd age group larvae. Similar results have been reported for other members of this genus (Hafez 1951, Lewis 1970). Putter and Thewke (1969) showed that

Table 1. Percent parasitization by *M. manilae* of fall armyworm larvae

Age group (hrs)	Test numbers[a]/ 1	2	3	4
1 (24-48)	24.5 a	26.7 a	26.7 a	13.2 a
2 (49-72)	28.3 a	30.1 a	27.8 a	11.4 a
3 (73-96)	22.5 a	20.7 b	19.5 b	12.3 a
4 (97-130)	6.9 b	5.2 c	6.8 c	3.5 b
Total	369	418	521	279

[a]Percentages followed by the same letter in the same column are not significantly different by Duncan's Multiple Range Test (P = 0.05).

M. feltiae preferred 1st to 3rd instar larvae (1st to 3rd age groups) of its host Agrotis ipsilon (Hufnagel) and Harcourt (1960) demonstrated a similar instar preference for M. plutellae Muesebeck and its host the diamond back moth Plutella maculipennis (Curtis). In contrast, Shepard et al. (1983) reported that M. demolitor (Wilkinson) preferred 3rd or 4th instar larvae of Heliothis spp. However, larvae of this size displayed a vigorous defense response and often damaged or destroyed the parasitoid. We observed also that when M. manilae females attempted to oviposit in 4th age group larvae that these larvae aggressively attempted to thwart the ovipositional attempt by swinging their heads and thoraxes from side to side in an attempt to bite the parasitoid.

The larval and pupal developmental times for M. manilae were similar for age groups 1-3 (Table 2). Egg to pupa and pupa to adult developmental times for M. manilae parasitizing 4th age age group hosts increased by approximately 2 days. Significantly more male progeny were produced from the 1st age group in contrast to the 2nd group from which more female progeny emerged. No significant differences were present in the sex ratios of progeny from 3rd or 4th age group larvae. The highest and lowest proportions of female progeny were observed for age groups 2 and 4, respectively. Bryan et al. (1969) showed that the

Table 2. Developmental periods (X ± S.E.) and progeny sex ratios for *M. manilae* in fall armyworm larvae

Age group (hrs)	Hosts exposed	Developmental period (days) Egg-pupa	Pupa-adult	Total	Sex ratio (%)[a] Males	Females
1 (24-48)	106	10 ± 2.3	4 ± 0.7	14 ± 3.0	62.5---*--37.5	
2 (49-72)	127	10 ± 2.9	3 ± 0.9	13 ± 3.8	42.9---*--57.1	
3 (73-96)	93	10 ± 2.1	4 ± 1.1	15 ± 3.2	46.8--ns--53.2	
4 (97-130)	43	12 ± 1.9	6 ± 1.7	18 ± 3.6	46.7--ns--55.3	

[a]Asterisk indicates significance at the 5% level by Student's *t*-test.

sex ratio of emerging progency of M. croceipes was approximately 1:1 when reared at 25°C. Only a single M. manilae emerged per host larvae irrespective of the age group parasitized. Bryan et al. (1969) reported an occasional emergency of 2 M. croceipes adults from a single Heliothis spp. larvae. Emerging M. manilae larvae appeared to perfer a dry surface on which to pupate and would frequently form cocoons on the underside of the lid rather than on the moist diet surface.

Male and female longevity was about 6-7 days. Mating increased female longevity to approximately 10 days. An increase of approximately 10% in parasitization was observed when the host exposure period for M. manilae females was increased from 15 to 30 min. (Table 3). Host exposure periods longer than 30 min. did not increase significantly the parasitization rate.

Biological knowledge about this parasitoid is necessary in any attempt to establish M. manilae as an additional mortality agent in the overwintering range of FAW. Ashley et al. (1982) showed that the native parasites destroyed approximately 63% of each of the 1st 4 instars and parasitization rates followed closely the increase or decrease in FAW larval populations. Parasitization rates of 3.5-30.1% by M. manilae in FAW larvae were

Table 3. Percent parasitization of second age group fall armyworm larvae exposed to *M. manilae* for various amounts of time

Host exposure (min)	No. containers [a]	(% Parasitization) (X ± S.E.)[b]
15	8	13.0 ± 3.7 a
30	11	22.0 ± 3.1 b
45	13	26.0 ± 1.7 b
60	9	24.5 ± 1.6 b

[a] Two female parasitoids and 20 larvae/container.

[b] Means followd by the same letter are not significantly different ($P<0.05$) by Duncan's Multiple Range Test.

observed in the laboratory. The results of our research will be used to rear M. manilae and to support efforts to establish this parasitoid in the overwintering range of FAW.

INTERSPECIFIC COMPETITION BETWEEN PARASITOIDS OF THE FALL ARMYWORM

Introduction

The fall armyworm (FAW), Spodoptera frugiperda is a serious pest of many graminaceous crops throughout the southeastern United States. Average estimates of annual crop losses exceed $300 million (Mitchell 1979). Since overwintering occurs only in the southern portions of Florida and Texas (Lunginbill 1928), increasing FAW mortality within this range may lower the numbers of adults participating in this pest's northward migration each spring. Fifty-three species of parasitoids have been reared from field collected larvae (Ashley 1979).

Knowledge of parasitoid interrelationships within FAW larval populations will increase our understanding of the factors that affects the dynamics of this pest, as well as contribute the biological control efforts. In endemic host enemy associations, interspecific competition appears to play a crucial role in structuring the parasitoid guild (Force 1974), and may influence the entire natural enemy complex as well. Parasitoids of the FAW provide a

relevant model for the study of interspecific competition within the host larva because of similarities in their life cycles. Ashley et al. (1982) supports the concept of interspecific competition during parasitiod development by demonstrating the presence of a dependent density pattern in percent parasitization between Chelonus insularis Cresson and Temelucha difficilis Dasch.

The present study assesses interspecific competition between two species of larval parasitoids, Microplitis manilae (Ashm.) and Cotesia (=Apanteles) marginiventris Cresson, and an egg-larval parasitoid C. insularis. It also describes the host finding and ovipositional sequence for C. marginiventris for hosts already parasitized by C. insularis. In addition data are presented on host acceptance of M. manilae and C. marginiventris of larvae already parasitized by C. insularis.

Materials and Methods

Host eggs or larvae were obtained from a FAW colony maintained at 23-25°C, 74-78% RH and under a 14:10 LD photoperiod. Moth oviposition occurred on paper towels, a portion of which were subsequently cut into sections each having 50-60 eggs. All hosts utilized in an experiment came from the same egg mass to help ensure host uniformity. In all experiments, except the fourth, these paper sections were

placed in a plexiglas® cage (25 cm^3) and exposed to two female C. insularis (24-48 hrs old) for 24 hrs. Each mass was observed to verify that a C. insularis female had parasitized the eggs. Masses attacked by two or more females and eggs close to the edge of the paper section that were not parasitized were destroyed. The larval parasitoids emerged in plexiglass cages (25 cm^3) kept at 26 ± 1°C, 60-70% RH and under a 14:10 LD photoperiod with a fluorescent light intensity of 800 ft-c. Female parasitoids were held in these cages along with males for a minimum of 48 hrs. Unless otherwise indicated, female parasitoids were between 2 to 4 days old. Host exposure for the larval parasitoids lasted 24 hrs and was accomplished by placing parasitoids, FAW larvae, and 1.5 cm cube of FAW diet (Leppla et al. 1979) into a 50-ml container (7 x 10 cm diam) with two air vents (1.5 x 3.0 cm) located near the top on opposite sides. Parasitoids were supplied with honey and water after adult eclosion and during the ovipositional period. Following host exposure, FAW larvae were placed individually into 30-ml plastic cups that contained approximately 15 ml of diet. These cups were held in a growth chamber at 25° ± 1°C, 77-80% RH and under a 14:10 LD photoperiod.

Experiment 1. Ninety FAW exposed previously to C. insularis as eggs were divided into three equal groups.

Larvae in group one, were not exposed to C. marginiventris or M. manilae and served to measure parasitization by C. insularis. Remaining larvae were exposed as second instars (48 hrs old) to C. marginiventris (group two) or to M. manilae (group three). Treatments were replicated nine times. The percent successful parasitization and the fate of non-parasitized larvae were recorded.

Experiment 2. Twenty second-instar larvae exposed previously to C. insularis as eggs were exposed to either M. manilae or C. marginiventris in the plastic containers. Ten replicates were made. In the control treatment, larvae were exposed to either C. marginiventris or M. manilae without prior parasitization by C. insularis.

Experiment 3. Fall armyworm larvae exposed as eggs to C. insularis and unexposed larvae were kept in separate plastic containers until the larvae were 3 days old. The ten exposed and ten unexposed larvae were transferred to new plastic containers. Two females of either C. marginiventris or M. manilae were introduced into a container for 30 min and the number of encounters, antennal examinations, ovipositor probes with and without cuticle contact were recorded. An encounter was defined as the arresting of random locomotion that resulted from sensing the FAW larva. An examination occurred when antennal palpation of the larvae by the parasitoid was observed. A probe was

observed. A probe was recorded when the parasitoid thrusted its ovipositor toward the larval cuticle. Finally, an apparent oviposition took place when the parasitoid mounted the host and inserted its ovipositor. Three replicates for each parasitoid species and larval combination were examined. Further replication was not possible because of the loss of the M. manilae colony.

Experiment 4. Eight host larvae derived from one of the following four groups were placed in a glass petri dish (15 x 100 mm diam): (1) initially parasitized by C. marginiventris and subsequently exposed to M. manilae; (2) initially not exposed to parasitoids and subsequently exposed to M. manilae; (3) initially parasitized by M. manilae and subsequently exposed to C. marginiventris; and (4) initially not exposed to parasitoids and subsequently to C. marginiventris.

As hosts were attacked they were removed and replaced with fresh larva. Non-parasitized larvae served as a control. The number of host encounters, examinations and apparent ovipositions were recorded. Five replicates for each species combination were run starting on the same day hosts were parasitized and then repeated 3 and 6 days later.

Experiment 5. The host finding behavior of C. marginiventris was investigated using 4-week-old corn, sorghum, Bermudagrass (Cynondon dactylon (L.)), and itch

grass. These plants were grown in pots (14.5 x 15 cm diam) containing a mixture of sand, perlite and peat moss (1:2:2 ratio, respectively). Supplementary nutrients were supplied with fertilizer (8-8-8 plus trace elements). FAW larvae exposed previously to C. insularis were allowed to become second instars. Plants were placed in wire cages (40 cm^3) in a greenhouse at 26-28°C, 70-75% RH and 14:10 LD photoperiod. Thirty larvae were placed randomly on the plant leaves. After 24 hrs, a female was introduced into the cage and her host finding behavior observed. Forty females were observed in sequence, their responses recorded and synthesized subsequently into common behavioral patterns.

Parasitization by C. marginiventris on FAW larvae also was measured on all four host plants. Thirty, second-instar larvae already parasitized by C. insularis were placed randomly into the plants. After 24 hrs of host larval feeding, two female C. marginiventris were introduced. The host larva were removed at 20-, 40-, 60-, and 80-min intervals. Three replicates for each time interval and plant species were made. Larvae were removed from the plants and placed in 30-ml cups to determine parasitization rates.

Results and Discussion

Experiment 1. Results of interspecific competition demonstrated that C. insularis was significantly more competitive than M. manilae (Fig. 1.) However, when C. marginiventris replaced M. manilae within the host larva, then C. marginiventris emerged more frequently than C. insularis. The combined parasitization rates for the three treatments ranged from 73-78%, which demonstrated that multiple parasitization did not seem to affect FAW larval mortality. FAW larvae parasitized by any two of the three parasitoid species only produced a single parasitoid, which suggests the destruction of one parasitoid larva by another. Salt (1961) and Vinson and Ables (1980) reported that when multiple parasitism occurred, all but one species was usually eliminated through physical attack, physiological suppression, or both. In a few instances, especially with gregarios parasitoids, some individualy of both species may survive (Miller 1982, Weseloh 1983).

Substantial differences were not present between the three parasitoid treatments for (1) larvae that successfully pupated and emerged as adults, (2) larvae that starved because they did not feed on the diet, (3) larvae that died from unknown causes and (4) larvae that fed on the diet but did not pupate (Table 4). Rejection of the

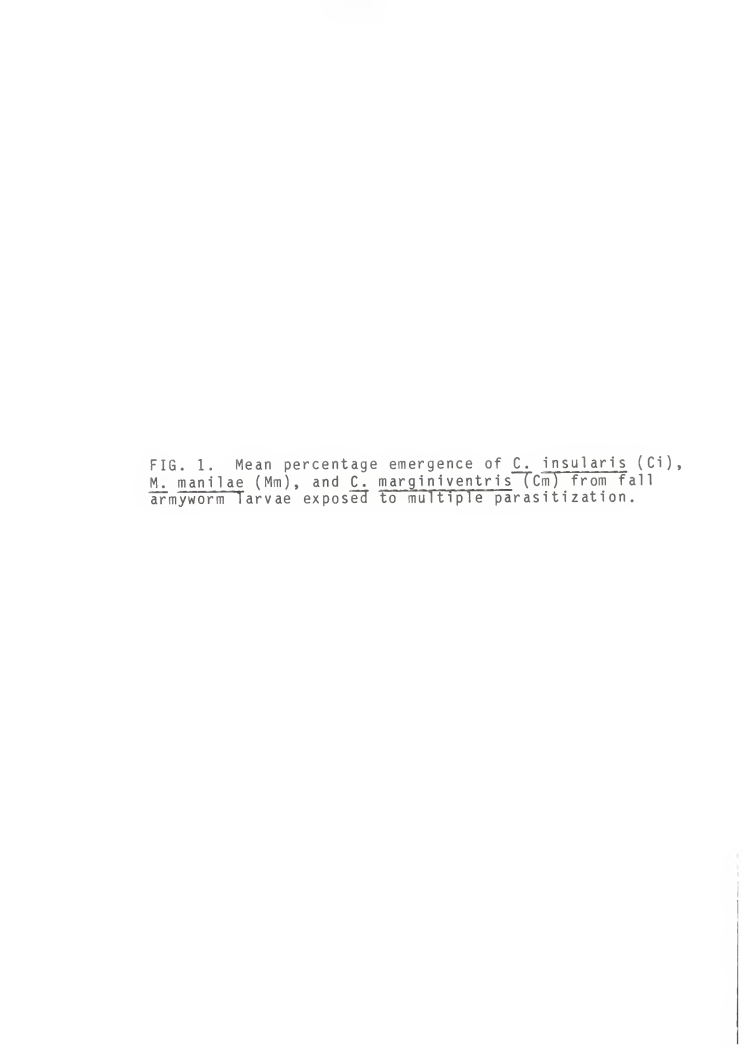


FIG. 1. Mean percentage emergence of C. insularis (Ci), M. manilae (Mm), and C. marginiventris (Cm) from fall armyworm larvae exposed to multiple parasitization.

% MEAN EMERGENCE OF PARASITOIDS
80
70
60
50
40
30
20
10
0
Ci
Mm
Cm
Ci & Cm
Ci & Mm
Ci - only
TREATMENT

Table 4. Mean percentages for emergence of Chelonus insularis (Ci), Microplitis manilae (Mm), Cotesia marginiventris (Cm) and adult FAW, and percentages for FAW larvae failing to mature because they refused to feed on the diet, for dying from unknown causes, and for failing to pupate[a]

Treatment	Parasitoid emergence			FAW	Refused diet	Unknown causes	Did not pupate[b]
	Mm	Cm	Ci				
Ci x Mi	13.7a		64.3a	7.0a	3.9a	5.8a	5.4a
Ci x Cm		46.0b	27.4b	8.7a	4.0a	7.7a	6.5a
Ci only			74.4a	7.3a	4.3a	7.7a	5.9a

[a]Treatments replicated nine times with 30 larvae/treatment. Means in the same column followed by the same letter were not significantly different by Duncan's Multiple Range Test (P = 0.05). This means for Mm (Column 2) and for Cm (Column 3) were compared using students t-test.

[b]Had not pupated by the time nonparasitized larvae had emerged.

larval diet may be one of the sources of artificial selection encountered when an insect population is placed under laboratory colonization (Boller and Chambers 1977). However, reasons for those larvae that fed on the diet but did not pupate or molt during the allocated period were not properly understood. Beckage (1982) observed Manduca sexta (L.) larvae parasitized by Apanteles smerrintie Riley often molted to larval-pupal intermediates even when parasitoids failed to emerge.

Experiment 2. The proportions of C. marginiventris and M. manilae adults that emerged from parasitized and non-parasitized hosts were not different significantly (Table 5). Cotesia marginiventris parasitized significantly more hosts then M. manilae. Larvae that were not parasitized by either parasitoid and emerged as FAW adults displayed significant differences in all four treatments. These data support the results of experiment 3, where M. manilae females altered their ovipositional behavior toward hosts already parasitized by C. insularis. Cotesia marginiventris did not appear to discriminate against hosts parasitized previously by C. insularis as there were no significant differences between C. insularis x C. marginiventris and C. marginiventris only treatments. Vinson and Iwantsch (1980) did not discriminate against C. insularis parasitized tobacco budworm hosts and neither did M. croceipes.

Table 5. Mean percentage emergence for Cotesia marginiventris (Cm) and Microplitis manilae (Mm) from FAW larvae exposed and not exposed as eggs to Chelonus insularis (Ci) and percents for emergence of FAW adults, larvae dying because they refused to eat the diet, and larvae not pupating.

Treatment	Mean emergence Ci	Cm	Mm	FAW	Refused diet	Did not pupate[b]
Ci x Cm	32.5	56.5		5.0	0.0	0.0
Cm only		52.5		30.0*	4.3	6.3
Ci x Mm	48.0		37.5	13.0	0.0	0.5
Mm only			44.5*	28.5*	11.5	16.5*

[a]Treatments replicated nine times with 20 larvae/treatment. Data analyzed by Student's t-test (* = significantly different at the 5% level).

Comparisons only made between treatments 1 ant 2, and 3, and 4. The means for Ci in treatments 1 and 2 were not compared statistically.

Experiment 3. The behavior of M. manilae females were altered significantly when exposed to hosts parasitized previously by C. insularis (Table 6). This altered behavior occurred in three categories; examinations, probes, and apparent oviposition. A similar behavioral pattern was not found for C. marginiventris. This indicated that C. marginiventris either cannot discern the presence of C. insularis in the host or that the presence of C. insularis does not inhibit oviposition. Vinson and Ables (1980) reported that tobacco budworm larvae parasitized previously by C. insularis also were acceptable to larval parasitoids Microplitis croceipes Cresson and Campoletis sonorensis Carlson as ovipositional sites.

Experiment 4. The number of encounters, examinations, and apparent ovipositions for the two larval parasitoids were not significantly different regardless of the parasitization sequence or the number of days between host exposure periods (Table 7). Initially, M. manilae made greater numbers of encounters in C. marginiventris parasitized larvae than in non-parasitized larvae. There was a trend for M. manilae to be more active with respect to encounters, examinations and ovipositions on hosts parasitized by C. marginiventris compared to non-parasitized hosts. Cotesia marginiventris was more active also on hosts parasitized previously by M. manilae than on

Table 6. Mean and percents for encounters, examinations, oviposition probes and apparent ovipositional success by Cotesia marginiventris and Microplitis manilae in fall armyworm larvae exposed and not exposed as eggs to Chelonus insularis.

Exposure to C. insularis	Mean[a]			
	Encounters	Examinations	Probes	Ovipositions
	Microplitis manilae			
Exposed	8.4	2.0	2.2	1.2
	(60.8)	(14.4)	(15.9)	(8.7)
Not Exposed	8.8	3.8*	4.2*	2.6*
	(45.5)	(19.6)	(21.7)	(13.4)
	Cotesia marginiventris			
Exposed	12.8	5.8	2.6	2.8
	(54.3)	(22.4)	(11.2)	(12.1)
Not exposed	14.2	5.8	2.9	2.9
	(55.04)	(22.5)	(11.2)	(11.2)

[a]Student's t-test analyzed at a = 0.05 level. Percents are in parentheses and are based upon the total number of behavioral observations (encounters + exams + probes + oviposition).

Table 7. Mean for numbers of encounters, examinations and apparent ovipositions by Cotesia marginiventris (Cm) and Microplitis manilae (Mm) during two host exposure periods separated by different numbers of days.

Host exposure		Days between host exposure period	Second host exposure means[a]		
First	Second		Encounters	Examinations	Apparent oviposition
Cm	Mm	0	13.2	7.8	6.8
None	Mm		11.8	6.9	5.6
		3	10.8	4.2	3.6
			9.6	5.4	3.0
		6	10.6	8.8	4.6
			9.8	8.0	4.0
Mm	Cm	0	11.4	8.8	6.6
None	Cm		9.6	7.8	6.0
		3	15.6	9.6	5.6
			14.4	8.8	5.2
		6	16.8	6.9	7.8
			17.4	6.8	7.0

[a]None of the number pairs were significantly different by Student's t-test.

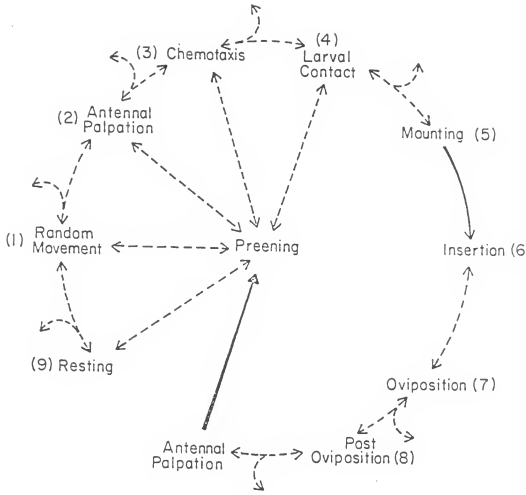
non-parasitized hosts. M. manilae had greater ovipositional contacts with the hosts that contained C. marginiventris larvae than C. marginiventris with host that contained M. manilae larvae on the first day of host exposure. This trend reversed itself on days 3 and 6.

Experiment 5. The host finding and behavioral sequence for oviposition of C. marginiventris on FAW larvae already parasitized by C. insularis on corn, sorghum, Bermudagrass and itch grass consisted on nine basic components (Fig. 2). During the sequence, preening occurred at several different steps. A typical pattern involved the following:

1. Random movement--The parasitoid female flew and walked randomly inside the cage or on the plant leaves. The upper portion of the leaf was preferred. The female held her antennae close and parallel to the substrate, or folded them back under her body.

2. Antennal palpation--The female started antennal palpation of the surrounding leaves and on the substrate. She held her antennae nearly parallel to the substrate and lowered her flagella slightly and raised them back to the horizontal position. This movement of the flagella frequently lasted for 5 to 25 sec. The under surface of the leaf was palpated more frequently.

FIG. 2. Behavioral ethogram of the host finding and ovipositional sequence of C. marginiventris females on fall armyworm larvae already parasitized by the egg-larval parasitoid C. insularis. (Solid arrows indicate invariable pathways and dashed arrows represent alternate pathways.)


(3) Chemotaxis
(4) Larval Contact
(2) Antennal Palpation
Mounting (5)
(1) Random Movement
Preening
Insertion (6)
(9) Resting
Oviposition (7)
Antennal Palpation
Post Oviposition (8)

3. Chemotaxis--The parasitoid became oriented and walked rapidly toward the site where FAW larvae feeding on the leaves. She vibrated her wings frequently and moved her body in a manner that indicated excitement.

4. Larval contact--Locomotion was arrested and antennal palpation of the host began with the apical portions of both antennae.

5. Mounting--The parasitoid jumped quickly onto the host, usually near the posterior portion.

6. Insertion--Stinging was performed immediately after the process of mounting. The wings were extended during the process.

7. Oviposition--This occurred immediately after insertion and the parasitoid moved away quickly from the host.

8. Postoviposition--The parasitoid restarted antennal palpation of the substrate. The female began an integrated sequence of abdominal bending and metathoracic leg extension. Preening always occurred.

9. Resting--The parasitoid was motionless.

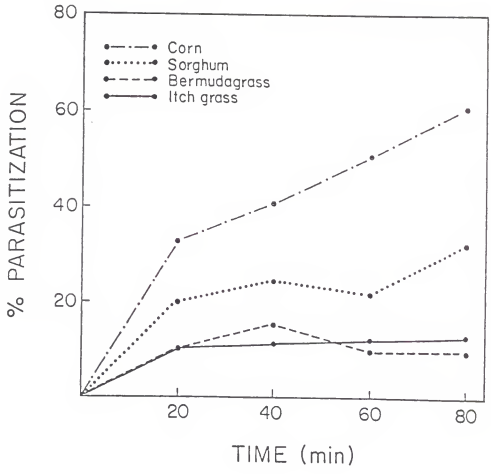
Loke et al. (1983) described the behavioral sequence of C. marginiventris on FAW damaged corn plants with an ethogram that consisted of 13 defined steps and divided the pattern of host finding behavior for C. marginiventris on non-parazitized FAW larvae into four phases:

non-searching movement, searching, oviposition, and resting. Analysis of our ethogram and that of Loke et al. (1983) showed that the elimination of certain steps in our ethogram are of particular interest because chemical cues from the earlier oviposition by C. insularis may have altered the behavioral pattern of the female C. marginiventris after ovipositing in an already parasitized FAW larvae.

The percent parasitization by C. marginiventris showed more than a two-fold increase in corn compared to sorghum and more than a four-fold increase over Bermudagrass and itch grass (Fig. 3). Sixty percent of the larvae were parasitized by C. marginiventris in corn after an 80-min host exposure period. There was no increase in parasitization for Bermudagrass and itch grass after 20 min. Ashley et al. (1983) found that parasitization rates for C. insularis and Temelucha spp. were substantially higher in corn than in Bermudagrass and paragrass Brachiarie mutica (L.). Cotesia marginiventris parasitized the highest proportion of hosts in Bermudagrass and paragrass. The differences in parasitization rates between these parasitoids may reflect a host plant preference (Ashley et al. 1983).

In our study, M. manilae apparently failed to compete successfully within the host larva when this larva contain

FIG. 3. Percentage parasitization by C. marginiventris of fall armyworm larvae already exposed as eggs to C. insularis. Larvae were randomly placed on four plant species held in wire cages within a greenhouse.


80
60
40
20
% PARASITIZATION
Corn
Sorghum
Bermudagrass
Itch grass
20
40
60
80
TIME (min)

a developing C. insularis. The possibility also existed that M. manilae recognized a previously parasitized host and failed to oviposit. Larvae parasitized as eggs by C. insularis caused a significant reduction in the number of host contacts, examinations, and apparent oviposition by M. manilae. Cotesia marginiventris oviposited in both C. insularis parasitized and nonparasitized larvae and was superior internal competitor compared to C. insularis. Exposing FAW larvae that have been parasitized as eggs by C. insularis to C. marginiventris or M. manilae did not result in additional larval mortality. If this same situation exists under field conditions, then C. insularis may be the key regulator of FAW larval populations.

EFFECT OF HOST AGE, PARASITOID AGE AND CHANGE OF TEMPERATURE ON INTERSPECIFIC COMPETITION BETWEEN CHELONUS INSULARIS CRESSON, COTESIA MARGINIVENTRIS CRESSON AND MICROPLITIS MANILAE ASHMEAD IN FALL ARMYWORM

Introduction

The fall armyworm (FAW), Spodoptera frugiperda occurs year-round in the tropical and subtropical areas of the western hemisphere, where it feeds on corn, sorghum, Bermudagrass and other members of the family Graminae. Damaging populations of FAW occur irregularly, and conditions conducive to outbreaks are not well understood (Barfield 1980). Estimated losses attributed to FAW reached $300 million in the southeastern United States during 1977, one of the most severe outbreak years (Sparks 1979).

A very diverse complex of natural enemies, especially parasitoids, attack the larval stages of FAW (Ashley 1979). The potential for interspecific competition exists between these parasitoids because more than one species attacks the same instar. Pemberton and Willard (1918) suggested that competition between parasitoids may prevent them from regulating their hosts effectively.

Ashley et al. (1982) reported the presence of a mirror image pattern with respect to percent parasitization of FAW larvae by the larval parasitoids, Chelonus insularis Cresson and Temelucha difficilis Dasch. and suggested that interspecific competition may have cuased this pattern.

Factors such as host age and environmental temperature affect the outcome of interspecific competition and evaluation of these factors should be of primary concern before initiating parasitoid release programs against a common host. A literature search provided no information on the effect of host age and temperature on competition among FAW parasitiods. Therefore, we selected the larval parasitoids Microplitis manilae Ashmed. Cotesia (Apanteles) marginiventris Cresson and the egg-larval parasitoid C. insularis for our investigations. These two parasitoids are among the principal natural enemies regulating FAW populations in southern Florida (Ashley et al. 1983). The specific objectives of our study were to determine the effects of host age, temperature and the age of C. marginiventris on interspecific competition.

Materials and Methods

Parasitoids were kept in plexiglass cages (50 x 50 x 24 cms) at 26 C,60-65% RH and under a 14:10 LD photoperiod

regime with a fluorescent light intensity of 800 ft-c and were supplied with honey and water. Adults of C. margini-ventris and C. insularis came from laboratory colonies established from FAW larval collections made from corn at Hastings and Homestead, Florida, respectively (Ashley 1983). Unless otherwise noted, parasitoids were 24-48 hrs old when used. The FAW host eggs were obtained from female moths maintained in a growth chamber set at 26-27°C, 70-75% RH and with a 14:10 LD photo regime. Host eggs were seperated using the technique of Gross et al. (1981). All eggs utilized in the experiments came from the same egg mass to help insure host uniformity. A grid was drawn on filter paper and individual eggs were placed in the center of each square. In all experiments FAW eggs were exposed initially to two female C. insularis inside a circular plastic container (7 x 10 cm diam) with 2 screened vents (1.5 x 3.0 cm) and containing 4 cubes (1.5 cm) of FAW diet (Leppla et al. 1979). Eggs attcked by two or more females and unparasitized eggs were destroyed. The grids were then cut into squares and suspended in a plastic container like those used for oviposition by C. insularis until egg hatch. These containers were kept inside an environmentally controlled cabinet set at 27°C, 70% RH, with a 14:10 LD photophase. When the FAW larvae were 48 hrs old (all were second instars) they were

exposed to two female C. marginiventris for 24 hrs inside a plastic container which was similar to the one used for C. insularis. The host larvae were then placed inside 30 ml plastic cups containing approximately 15 ml of diet. These cups were sealed with paper lids and placed inside the cabinet. The larvae remained in these cups and their fate recorded. The control treatment for experiments 1 and 2 consisted of larvae exposed only to C. marginiventris.

Experiment 1--Host Age

Forty second instar FAW larvae (head capsule width 0.4-0.5 mm) were transferred to an ovipositional unit at 12, 24, 36, 48, 60, 72, and 84 hrs of age and exposed to two female C. marginiventris for 24 hrs. Each age was replicated seven times.

Experiment 2--C. marginiventris Age

Cotesia marginiventris cocoons were held for adult sclosion and mating inside a plastic container similar to the one used for C. insularis oviposition. When C. marginiventris parasitoids were 24, 48, 72, 96, and 108 hrs old, two females were exposed for 24 hrs with 40 second instar FAW larvae. Treatments were replicated seven times.

Experiment 3--Temperature Effects

Thirty second instar FAW larvae were exposed to two female C. marginiventris for 24 hrs. These experiments

were conducted in plastic containers like those used for oviposition by C. insularis. After exposure to C. marginiventris, larvae were placed individually in 30 ml plastic cups and held at the following temperatures 19, 22, 25, 28 and 31°C and RH 75-78% with a 14:10 LD photophase. Each treatment was replicated seven times. A control treatment was run at 26°C with host larvae exposed only to C. insularis. The cups were checked three times a week and larval fate recorded.

In a second portion of this experiment larvae emerging from eggs parasitized by C. insularis were exposed to C. marginiventris when reaching the following host ages (hrs) 6-10, 12-18, 24-30, 36-42 and 48-54. After exposure to C. marginiventris, larvae were individually placed into 30 ml cups and held at the temperatures cited above. Treatments were replicated six times. The control treatment was held at 26°C and the RH ranged between 70-75%.

Experiment 4--Dissection of Multiparasitized Hosts

Host exposure to C. insularis followed by exposure to C. marginiventris or M. manilae were performed as previously described. The C. insularis - C. marginiventris parasitized larvae were then placed inside a plastic container for 3, 5, 7 or 9 days. The C. insularis - M. manilae parasitized larvae were similarly held for

3, 6, 8, or 10 days. Twenty to thirty host larvae were dissected at the end of each time period to determine the condition of the competing parasitoids. In the nine day treatment, C. marginiventris larvae had emerged before dissections were done. However, since the host was still alive it was dissected to determine the fate of the immature C. insularis. The descriptions of Boling and Pitre 1970) and Glogoza (1980) were used to recognize larvae of C. marginiventris and C. insularis, respectively.

Results and Discussion

Thirty six hr old FAW larvae produced the highest proportion of C. marginiventris and lowest proportion of C. insularis (Table 8). Emergence of C. marginiventris showed significant differences between 60 and 72 hrs and 24 and 36 hrs but there were not significant differences between 12 and 24 hrs, and 72 and 84 hrs. There was not significant difference in emergence of C. marginiventris from hosts 36 hrs old and the control. Loke and Ashley (1984) reported that highest rate of parasitization by C. marginiventris of FAW occurred in 48 hr old larvae (second instars). Kunnalaca and Mueller (1979) and Boling and Pitre 1970) stated that females of C. marginiventris produced the most progeny from 2 and 3 day old hosts. Larvae less than 24 hrs did not produce as many

Table 8. Mean percentages at different host ages for emergence of Chelonus insuaris (C.i.) Cotesia marginiventris (C.m.) and adult fall armyworm and percent mortality of FAW larvae due to (1) refused to feed on the diet, and (2) died from unknown causes.a/

Host age b/ (hrs)	Percent Parasitoid emergence			FAW mortality	
	C.i.	C.m.	FAW	Refused diet and diet	Unknown causes
12	25.5a	20.7a	45.2a	7.4a	1.1a
24	30.4a	15.7a	35.0b	12.2a	6.7ab
36	17.6a	44.2b	20.3c	13.2a	4.8ab
48	18.8a	40.1bc	16.2cd	17.4a	7.5ab
60	31.7a	32.9c	14.3cd	14.1a	6.9ab
72	52.7b	17.6a	14.8cd	11.7a	3.1ab
84	45.9b	15.2a	10.6d	18.7a	9.6b
Control	-	45.2b	25.6b	15.8a	8.5b

a/ Treatments were replicated 7 times with 40 larvae per treatment. Means followed by same letter for a given column are not significantly different by Duncans Multiple Range Test. (P = 0.05).

C. marginiventris as larvae between 36 and 48 hrs. Chelonus insularis emerged more successfully than C. marginiventris from larvae 12 and 24, and 72 and 84 hrs old. Emergence of C. insularis in early and latter ages of the host was expected because in most cases of multi-parasitism the first species that attacked the host was more successful than the second species (Doutt and De Bach 1964). The emergence pattern of C. insularis showed significant differences between larvae 60 and 72 hrs old. This difference was probably a function of the larger larvae becoming less suitable for parasitization by C. marginiventris. The percentage of non-parasitized larvae that became adults was greater except at 48 and 84 hrs than those that died from unknown causes or starved to death. There was a steady decrease in the percent larvae that became FAW adults as host age increased. Substantially more larvae died refusing to eat the diet and died than from unknown causes. No significant differences were found between host ages for larvae dying from refusing to feed. This rejection of larval diet may be a source of artificial selection encountered when an insect population is placed under laboratory colonization (Boller and Chambers 1977). Ashley et al. (1982) reported that a definite proportion of the FAW larval population refused to feed on the artificial diet and that diet rejection was not restricted to the early instars. Significant

differences were observed for larvae dying from unknown causes between 12 and 24 hrs and 72 and 84 hrs of age.

Experiment 2--C. marginiventris Age

C. marginiventris adults which were 48 to 96 hrs old produced more parasitoids than did those 24 or 108 hrs old (Table 9). There were no significant differences in emergence of C. insularis at 24 and 108 hrs suggesting that C. marginiventris was either too young or too old to start egg laying. There were no significant differences between the control and 48, 72 and 96 hrs which indicated that the presence of a C. insularis larva inside the host did not reduce oviposition by C. marginiventris. Mean parasitization for all ages illustrated that C. insularis had a higher parasitization level (45%) than C. marginiventris (41%). Wallner (1982) reported that when two parasitoids attack the same host the parasitoid ovipositing in the host first was more successful. Significant differences were observed for emergence of C. insularis at all the ages studied. However, highest emergence for C. insularis occured at 24 and 108 hrs.

Deaths due to unknown causes ranged from approximately 2.00 to 7.5 percent with the most mortality occuring in the 108 hr treatment and control. A substantially high proportion of larvae refused to eat the diet in 96, 108 hrs and control treatments.

Table 9. Mean percentages for emergence of Chelonus insularis (C.i.), Cotesia marginiventris (C.m.) and adult FAW and percent mortality for FAW larvae due to (1) refused to feed on the diet, (2) dietd from unknown causes, when age of C.m. was changed a/

C.m. age b/ (hrs)	Percent Parasitoid emregence			FAW mortality	
	C.i.	C.m.	FAW	Refused diet and diet	Unknown causes
24	58.5a	33.6a	2.9a	2.9a	2.0a
48	39.3b	52.5b	2.1a	3.2a	2.9ab
72	42.4bc	47.4b	1.4a	4.9ab	3.9ab
96	30.6b	48.7b	2.1a	13.7c	5.4ab
108	54.5a	21.0c	5.9a	11.0bc	7.7b
Control	-	55.0b	9.9a	14.8c	10.1b

a/ Treatments were replicated 7 times with 40 larvae per treatment. Means followed by same letter for a given column are not significantly different by Duncans Multiple Range Test. (P = 0.05).

Male progeny were always in greater abundance in C. marginiventris regardless of parental age (Fig 4). Boling and Pitre (1970) reported that mated C. marginiventris generally produced with a sex ratio of 1:1. However, only the 72 hr age group came close to this ratio. A very high percentage of female C. insularis emerged in 96 hrs (Fig 5) and a very large percent of males emerged from the 108 hr group. Sex ratios in hymenopterous parasitoids may be affected by suitable host abundance (Rechav 1978); however, the reason for the abrupt change of sex ratio of C. insularis in the 96 and 108 hr treatments was not properly understood. Mitchell et al. (1984) reported a significant shift in the sex ratio of C. insularis towards males in the field between April and October.

Experiment 3--Temperature effects

Cotesia marginiventris emerged most successfully at 25°C and it appeared that temperature affected the outcome of competition (Table 10). Significant differences between emergence rates were present for C. marginiventris at all temperatures except 28 and 31°C. There were no significant differences at 22, 25, 31 and 28°C for C. insularis but significantly more emerged at 28 than at 25°C. Less emergence was observed for both parasitoids at low temperatures while optimum temperatures for C. marginiventris and C. insularis were 25 and 31°C,

FIG. 4. Progeny sex ratios for C. marginiventris from different aged C. marginiventris (C.m.) emerging from fall armyworm larvae parasitized as eggs by C. insularis.

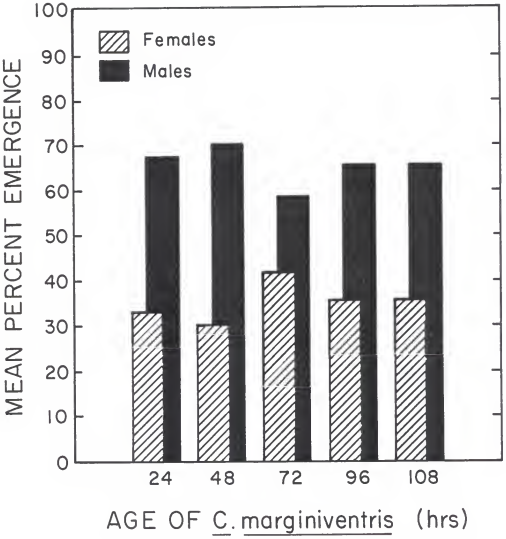

Females
Males
MEAN PERCENT EMERGENCE
100
90
80
70
60
50
40
30
20
10
0
24
48
72
96
108
AGE OF C. marginiventris (hrs)

FIG. 5. Progeny sex ratios for C. insularis (C.i.) from different aged C. marginiventris (C.m.) emerging from fall armyworm larvae parasitized as eggs by C. insularis.

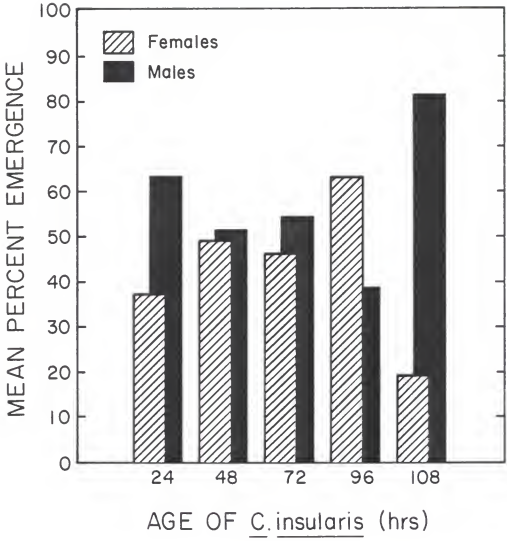

MEAN PERCENT EMERGENCE
100
90
80
70
60
50
40
30
20
10
0
Females
Males
24
48
72
96
108
AGE OF C. insularis (hrs)

Table 10. Mean percentages (± SE) when reared at several constant temperatures for emergence of Chelonus insularis (C.i.), Cotesia marginiventris (C.m.) and adult fall armyworm and percentages for FAW larvae failing to mature because they (1) refused to feed on diet and died, (2) died from unknown causes, (3) still larvae at end of test, and (4) escaped from cup a/

Temperature (°C)	Percent Parasitoid emergence			Refused diet and died	Unknown causes	Still alive	Escaped
	C.i.	C.m.	FAW				
19	10.3±1.5a	8.5±2.0a	8.2±1.9a	26.9±2.0a	15.5±3.4a	30.5±3.0a	3.3±1.4a
22	12.6±2.1a	18.6±1.9b	16.1±1.8a	34.4±2.7b	3.9±1.2b	14.2±3.2b	2.3±1.2a
25	13.6±2.6a	61.0±3.6c	15.5±3.9a	3.9±1.1d	6.0±1.8b	0.0±0.0c	1.9±1.2ab
28	34.4±2.0b	32.8±3.0d	15.2±1.4a	9.3±1.7c	7.8±1.4b	0.5±4.9c	1.8±1.2ab
31	38.9±1.8b	29.8±3.3d	14.9±3.0a	9.6±0.9c	6.8±1.5b	0.0±0.0c	1.5±1.0a
Control	35.5±1.4b	-	17.6±1.0a	10.3±0.8c	10.7±1.0b	1.5±1.1c	15.0±1.7c

a/ Treatments were replicated 7 times with 30 larvae/treatment. Means followed by same letter for a given column was not significantly different by Duncans Multiple Range Test. (P = 0.05).

respectively. Temperature did not affect emergence of FAW adults. A significant number of larvae were found to be alive at 19 and 22°C. There was a significant difference for larvae which died for unknown reasons at 19°C and the remaining temperatures.

The time required for development of C. marginiventris from oviposition to emergence as adults ranged from 12-20 days and declined as temperature increased (Table 11). The longest emergence period for both parasitoids occured at 19°C. Kunnalaca and Mueller (1979) reported the development time for C. marginiventris decreased between 25 and 30°C. The range of time required for C. insularis from oviposition to adult emergence was from 26 to 35 days. Significant differences were observed between 19 and 22°C for all parameters measured. An abnormally high number of larvae was unable to pupate at 19°C and development of the FAW was slower at the lower temperatures. Keller (1980) reported similar results.

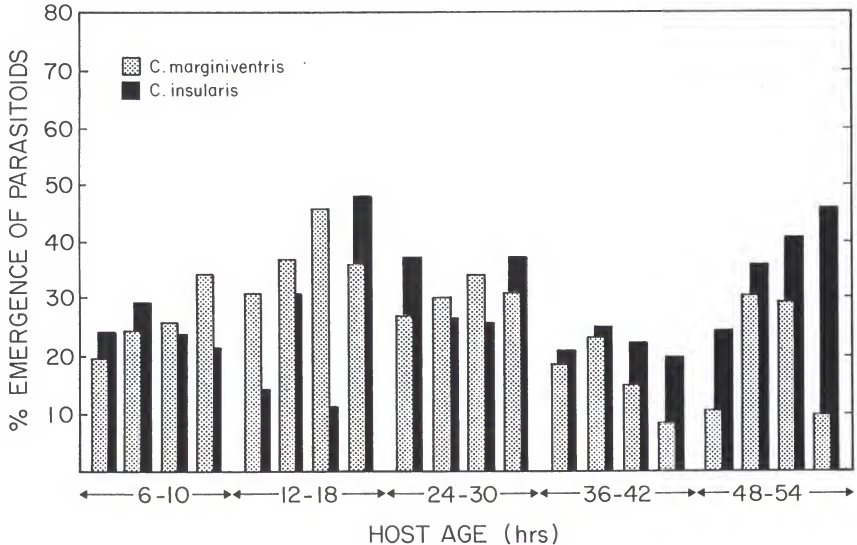
Cotesia marginiventris emerged more successfully than C. insularis when hosts were 12-18 hrs old at 19, 22, and 25°C (Fig 6). Chelonus insularis was more successful at host ages of 36-42 and 48-54 hrs under all temperatures indicating that C. marginiventris either did not prefer older hosts or was unable to develop in them successfully. Cotesia marginiventris was more successful with hosts at

Table 11. Mean (± SE) emergence periods (days) when reared at several constant temperatures for Cotesia marginiventris (C.m.) and Chelonus insularis (C.i.) and adult fall armyworm and percentages for FAW larvae failing to mature because they (1) refused to feed on the diet and died, (2) still larvae at end of test. a/

Temperature b/ (°C)	Percent Parasitoid emergence			Refused diet and died	Still alive
	C.i.	C.m.	FAW		
19	35.5±1.1a	20.1±1.2a	40.6±1.3a	3.5±1.0a	60.3±1.1a
22	30.3±1.6b	18.6±1.1b	34.5±1.1b	6.9±1.5b	30.3±1.7b
25	26.3±1.5b	17.3±2.1b	28.9±2.1c	1.5±1.7b	0.00c
28	27.5±1.9b	12.5±12.5b	19.5±1.3d	2.7±1.7b	0.00c

a/ Treatments were replicated 7 times with 30 larvae/ treatment. Means followed by same letter for a given column are not significantly different by Duncans Multiple Range Test. (P = 0.05).

FIG. 6. Percentage emergence of C. marginiventris and C. insularis from fall armyworm (FAW) larvae, parasitized on eggs by C. insularis. FAW larvae were exposed at different ages to C. marginiventris and then held at 19, 22, 25, 05 28°C for development.


80
70
60
50
40
30
20
10
% EMERGENCE OF PARASITOIDS
C. marginiventris
C. insularis
6-10
12-18
24-30
36-42
48-54
HOST AGE (hrs)

24-30 hrs old at 22 and 25°C than was C. insularis. In. general, C. marginiventris emerged from a higher proportion of younger hosts than did C. insularis. Hosts older than 36 hrs produced more C. insularis regardless of temperature. Two possible explanations for this are as follows: (1) C. marginiventris was a better competitor in younger hosts and (2) either oviposition or successful competition was reduced in older hosts larvae containing a developing C. insularis.

Experiment 4--Dissection of Multiparasitised Hosts

Dissections of multiparasitized larvae showed no evidence of physical attack between parasitoids during the first 5 days of host development (Table 12). However 7 days after parasitition, 5 C. insularis larvae had visible melanized scars, while those of C. marginiventris were unscared suggesting that C. marginiventris physically attacked larvae of C. insularis. Vinson and Ables(1980) reported that larvae of C. insularis had visible evidence of physical attack after 3 days in hosts parasitized by the larval parasitoid Campoleis sonorensis (Carlson). Six days after parasitization by M. manilae, 5 dead M. manilae larvae were found in the hosts. This number of dead larvae was higher at 8 and 10 days although there was no visible evidence of physical attack. Vinson and Iwantsch (1980) reported that M. croceipes mutilated the

Table 12. Fate of larval parasitoid C. marginiventris (C.m.) and M. manilae (M.m.) in competition with the egg larval and parasitoid C. insularis as determined by dissection of fall armyworm (FAW).

Competitor species	No. of FAW larvae dissected	After exposure to 2nd parasitoid when dissected	Fate of C. insularis	Fate of C. marginiventris or M. manilae
C.m.	26	3	23 larvae 3 no larvae	21 eggs 5 no larvae
	26	5	22 larvae 4 no larvae	19 larvae 7 no larvae
	20	7	5 injured larvae 15 larvae	4 injured larvae 16 larvae
	23	9	/c	3 larvae/a
M.m.	30	3	28 larvae 2 no larvae	26 egge 3 shriveled egge 1 no egg
	23	6	20 larvae 3 no larvae	5 dead larvae 12 healthy larvae 6 no larvae
	20	8	20 larvae	7 dead 10 healthy larvae 3 no larvae
	23	10	10 larvae 13 no larvae	10 dead larvae/b 2 no larvae

/a Most of C. marginivenris have formed cocoons.

/b Some larvae emerging from host to form cocoon outside.

/c C. insularis larvae were not found.

C. insularis larvae by physical attack and killed them in 5 days.

In summary, C. marginiventris reproduced most successfully in 36 hr old FAW larvae. C. marginiventris adults which were 48 to 96 hrs old produced the greatest number of parasitoids. C. insularis and C. marginiventris developed optimally at 31 and 25°C. Cotesia marginiventris physically attacked developing C. insularis larva inside the host. Dead M. manilae larvae were found in hosts multiparasitized by C. insularis and M. manilae but the cause of the death was unknown.

INTERSPECIFIC COMPETITION BETWEEN FALL ARMYWORM PARASITOIDS CHELONUS INSULARIS AND COTESIA MARGINIVENTRIS INSIDE FIELD CAGE AND PLOTS

Introduction

The fall armyworm (FAW), Spodoptera frugiperda, is one of the few argicultural pests infesting many members of the family Graminae in the United States. Each year the FAW migrate from tropical and subtropical areas to occupy a range which may extend northward to the Canadian border and westward to Montana. Major losses in late planted corn, sorghum and other susceptible crops are experienced when high populations of FAW are present. Mitchell (1979) estimated that if a severe outbreak occurred, as in 1977, losses could exceed $500 million. Ashley et al. (1982) reported that up to 63% of first 4 instars are destroyes by parasitoids of FAW.

Interspecific competition among parasitoids within the same host can have a significant impact on the host's population dynamics. The occurence of interspecific competition may result in the death of one or both parasitoid (Salt 1961). Therefore, this competition may be a vital component influencing the parasitoid guild

(Zwolfer 1970). Ashley (1979) recorded 53 species in 43 genera from 10 families having been reared from FAW larvae. Two of the most frequently recovered parasitoids in the FAW overwintering region in Southern Florida were, Cotesia (Apanteles) marginiventris Cresson which develops in FAW larvae, and Chelonus insularis (Cresson) which parasitizes the egg emerges during the larval stages of FAW (Ashley et al. 1982).

We performed 4 experiments in the evaluation of FAW/parasitoid interactions. The objective of the first experiment was to study the functional response of C. marginiventris when exposed to different densities of FAW previously parasitized by C. insularis. In the second experiment we examined the functional response of C. marginiventris to different levels of multiparasitized host densities inside the laboratory. In the third experiment data were obtained on the ovipositional preferences of these two parasitoids at different FAW densities inside field cages. The fourth experiment determined the impact of C. insularis and C. marginiventris on FAW larvae found in different regions of the plant and the surrounding environment.

Materials and Methods

Host and Parasitoid Colony Maintenance

A colony of the FAW was maintained at 23-25°C, 74-78% RH and under a 14:10 LD photoperiod. Adults were fed with 10% sucrose solution. Adult FAW oviposition occurred on paper towels that were subsequently cut into sections each having a single egg mass of 50-60 eggs. These sections were placed in circular plastic cups (7 x 10 cm diam) having two screened vents (1.5 x 3.0 cm). These cups were used as ovipositional units and contained 4 cubes (1.5 cm) of pinto bean diet (Leppla et al. 1979).

Adult C. insularis and C. marginiventris were held in plexiglasss cages (50 x 50 x 24 cms) at 26°C, 60-65% RH and 14:10 LD photo regime. Undiluted honey and water were provided to adult parasitoids. Unless otherwise noted, parasitoids were 1-4 days old when used for experimentation.

Experimental Procedures for Host Parasitization

Individual FAW eggs were isolated using the technique described by Gross et al. (1981). All eggs in each replicate, came from the same egg mass. A grid was drawn on filter paper and individual eggs were placed in the center of each square, inside a plastic petri dish (100 x 15 cm). The eggs were then exposed to two female C. insularis and any that were attacked more than once were discarded. After parasitization, eggs were kept in the plastic cups,

with FAW diet inside an incubator at 26+1°C, 75-80% RH and 24:00 LD photo regime, until the larvae emerged. When these larvae reached the second instar larvae (head capsule width 0.5-0.6 mm) they were exposed to two, C. marginiventris females in plastic petri dishes (100 x 15 cm) for 24 hrs. The larvae were individually placed in 30 ml plastic cups containing approximately 15 ml of FAW diet.

Corn variety (Pioneer x 304C) was planted at Homestead, Florida in inside field cage and in study plots. When the FAW larvae were second instars, female C. marginiventris were released into field cages and study plots each day between 1600 and 1800 hrs until the conclusion of the release period. Corn plants adjacent to the study plots were also sampled. Plants were individually taken apart and examined for FAW larvae. Head capsule widths were measured to determine larval instars (Ashley et al. 1982). Each larva was placed in a 30 ml plastic cup containing FAW diet. The cups were checked until the fate of each larva and the sex of each adult that emerged were recorded.

Experiment 1--Host Density. The FAW eggs were exposed to C. insularis at densities of 1, 2, 4, 8, 16, 32, and 64 in a plastic container. Second instar larvae were placed in the same container with FAW diet and were exposed to two C. marginiventris females at the same densities for 24 hrs. Treatments containing 1 larvae/cup

and 2 larvae/cup were replicated 10 times and the remaining treatments were replicated 7 times. FAW larvae were exposed to C. marginiventris at 24, 48, 72 and 96 hrs pf age. The larvae were transferred subsequently to 30 ml cups and their fate determined.

Experiment 2--Field Cages

Three field cages (246 x 155 x 115 cm) were contructed from metal pipe frames and screened with woven cloth netting so that insect activity could be observed. Each cage contained 20 corn plants, with 91.4 cm between rows and 8 inches between plants. Methonyl was applied at the rate of 10 ml/3.79 L 7 days before the introduction of host eggs. Four randomly selected plants were pinned to one, two or three paper sections (1.54 x 5.08 CM) containing 50-6 FAW eggs. The corn plants were approximately 4 weeks old and 75-85 mm in height and the egg masses were pinned to the lower surfaces of the upper leaves within 20.3 cm of the growing terminal. Twenty female C. insularis were released into each cage just prior to sunset followed by release of 20 C. marginiventris females on each of the next 3 days. The experiment was repeated 3 times over a 4 month period with 3 cages per replicate. Plants with paper sections were sampled 3 days after the final introduction of C. marginiventris and the remaining plants in the perimeter area were allowed to grow for 2 weeks prior to sampling.

Experiment 3--Field Plots

Corn was planted in six adjacent plots, (50 x 11 m) in the center of a field previously used to produce field corn. Each plot was disked twice before planting. Seven to ten days after disking corn seeds were planted at a depth of 3.0 cm and spaced 91.4 x 243.8 cm (between rows and plants). The plots were irrigated weekly and two week after planting ammonium nitrate fertilizer (33.5% N) was broadcast over each plot at a rate of approximately 165 kg/ha. Four to five weeks after planting, plants selected at random were pinned with a paper section having approximately 50-60 FAW eggs at the following locations: (US) upper surface of leaves (within 20.3 cm from terminal) (oriented less than 45° from stalk), (LS) lower surface of leaves (oriented more than 45° from the stalks,) (ST) stalk (central stem with a pithy core), (GS) ground (within 5.08 cm from the plant), (SH) in between stalk and leaf sheath (Fig 16).

The eggs were not washed. The five treatments were replicated 6 times within the plot. A control plot was left with FAW eggs pinned into the whorl region. Starting from the first day after egg pinning, 480 C. insularis females were introduced for 3 consective days. On the 4th day 498 female C. marginiventris were released. The complete experiment with 6 plots (5 with treatments + control) was replicated 3 times over a 4 month period.

A sample consisted of harvesting all the plants in a 10-m area.

Comparisons were made between parasitoid release plots and non release plots in terms of FAW larval damage to whorl (leaves surrounding the furl with blades partially extended and sheath concealed) and furl (leaves surrounding a central roll) and stalk. The plants with recongnizable FAW feeding in whorl, furl or stalk with FAW larvae present were defined as damaged.

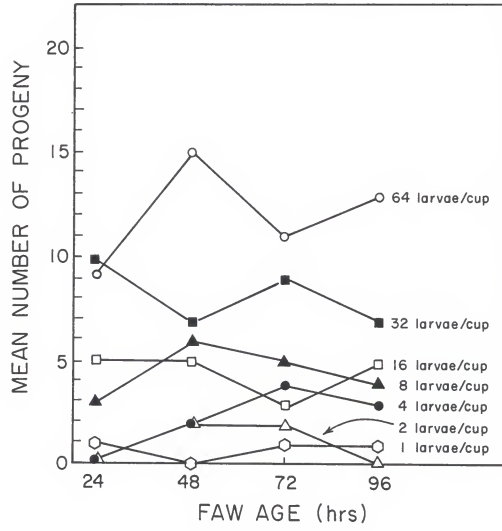
Results and Discussion

Experiment 1--Host Density

The mean number of C. marginiventris that emerged from densities of 64 and 32 larvae produced patterns that were almost mirror images of each other (Fig 7). A density of 64 larvae/cup represented the highest mean progeny production at 48 hrs. Kunnalaca and Mueller (1979) reported that C. marginiventris parasitized between 31 and 110 hosts each day. The greatest difference in progeny densities occurred between the 64 larvae/cup density and the remaining densities.

More superparasitism occured at 4 and 8 larvae than at 32 larvae suggesting that C. marginiventris exposed to lower densities attacked many hosts more than once. However at higher densities only one parasitoid emerged per host larvae which showed that C. marginiventris avoided

FIG. 7. Mean progeny production by C. marginiventris at 7 host densities from eggs previously parasitized by C. insularis.


MEAN NUMBER OF PROGENY
20
15
10
5
0
24
48
72
96
FAW AGE (hrs)
64 larvae/cup
32 larvae/cup
16 larvae/cup
8 larvae/cup
4 larvae/cup
2 larvae/cup
1 larvae/cup

superparasitism at high densities (Table 13). The longevity of emerging C. marginiventris was greater at lower densities than at higher densities. Substantially more larvae were found dead at higher than at lower parasitoid densities, probably due to cannibalism. (Ashley, Pers. Comm. 1985).

A similar trend of progeny production was observed for C. insularis (Fig 8). The 64 larvae/cup treatment had produced the highest number of progeny. The number of progeny were related to the parasitoid density. As the number of larvae per treatment was increased a consequent increase in progeny production was observed. This is a well recognized characteristic of many parasitic hymenoptera (Legner 1969). C. insularis was more successful in progeny production than C. marginiventris at higher densities. A number of events may have been responsible for the apparent success of C. insularis. The females spent less time examining eggs before ovipositing at the higher density. Also the female C. insularis oviposited more eggs at higher host density than at lower density. C. marginiventris may have detected hosts previously parasitized by C. insularis by some external stimuli and reduced oviposition. C. insularis received unparasitized eggs for oviposition. The reduction of oviposition by C. marginiventris may have helped for developing C. insularis larvae to emerge without a competition.

Table 13. Means (±SE) numbers of FAW hosts attacked at 7 densities by C. marginiventris.

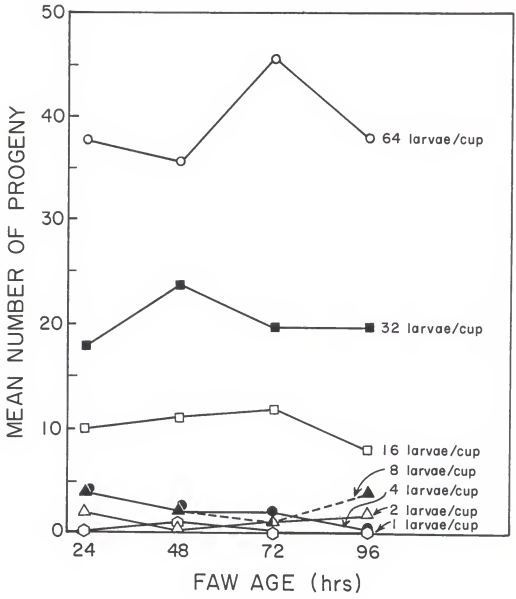
Mean numbers of	Host density[a] 1	2	4	8	16	32	64
Hosts super-parasitized	0.5± 0.1	1.1±0.01	1.3±0.2	1.3±0.02	1.1±1.2	1.0±0.02	1.2±0.05
Longevity of progeny	6.1±0.7	5.6±0.7	5.1±0.8	7.4±0.1	4.1±1.3	4.3±1.6	4.6±1.7
Survival of larvae	1±0.0	2±0.0	3.9±0.1	8.0±.07	15.3±0.7	29.7±07	54.2± 2.1

a/ Seven replications at each host density.

b/ Significant by student "t" test at P=0.05 level.



FIG. 8. Mean progeny production by C. insularis at 7 host densities and parasitized by C. marginiventris.


MEAN NUMBER OF PROGENY
50
40
30
20
10
0
24
48
72
96
FAW AGE (hrs)
64 larvae/cup
32 larvae/cup
16 larvae/cup
8 larvae/cup
4 larvae/cup
2 larvae/cup
1 larvae/cup

The sex ratio of C. marginiventris progeny favored females at densities of 2 and 4 larvae (Fig 9). The C. insularis males outnumbered females at all densities except at 4 eggs/larvae where 1:1 ratio was obtained (Fig 10). The presence of more females at low densities may be seen as a mechanism that ensures the presence of a minimum number of males to fertilize all the females. Such mechanisms have been reported in other parasitoids in which mated females are functionally virgin for a certain period of time after mating (Mackauer 1976).

Experiment 2--Field Cages

Chelonus insularis emerged most frequently in treatments having 1 or 2 paper sections while C. marginiventris was the major parasitoid in the 3 paper section treatment during the first and second test periods (Fig 5). In the last test period no definite emergence patterns were observed. The decrease in emergence of C. insularis in 3 paper section treatment indicated that C. marginiventris was a better competitor in crowded host conditions. Wiseman et al. (1983) reported that FAW larvae often moved from infested plants onto surrouding border plants during the 3 to 5 days after infestation. This movement may have aided C. marginiventris in locating hosts. C. insularis emerged more successfully in 1 and 2 paper sections and appeared to search the portions of corn plants where most FAW eggs were deposited. However, Loke and Ashley (1984)

FIG. 9. Sex ratio of C. marginiventris from 7 host densities.

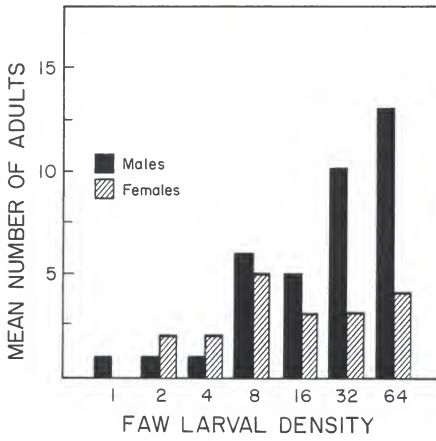

MEAN NUMBER OF ADULTS
15
10
5
Males
Females
1
2
4
8
16
32
64
FAW LARVAL DENSITY

FIG. 10. Sex ratio of C. insularis from 7 host densities.

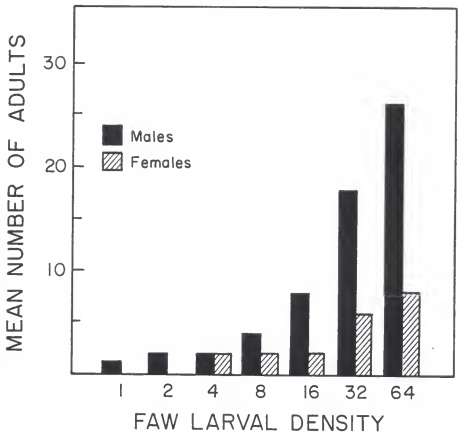
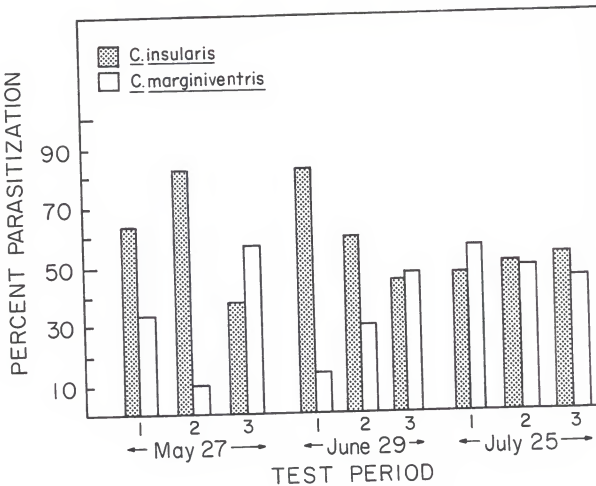

MEAN NUMBER OF ADULTS
30
20
10
Males
Females
1
2
4
8
16
32
64
FAW LARVAL DENSITY



FIG. 11. Percent parasitization by C. insularis and C. marginiventris from FAW larvae recovered inside from field cage during 3 test perids. Vertical bars within a test period from lest to right indicate treatments 1, 2, and 3 paper sections.

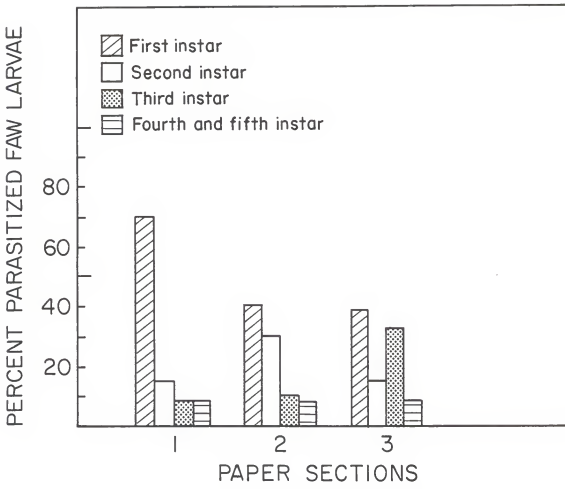

C. insularis
C. marginiventris
PERCENT PARASITIZATION
90
70
50
30
10
1
2
3
1
2
3
1
2
3
← May 27 →
← June 29 →
← July 25 →
TEST PERIOD

reported that C. marginiventris was a day adapted species and has been observed searching for hosts in bright sunlight in corn fields.

The release of two parasitoids inside the field cages resulted in an overall parasitization rate of 60.0% for C. insularis and 37.4% for C. marginiventris. This high rate of parasitization was similar to the field results reported by Mitchell et al. (1984) where C. insularis Temelucha difficulis Dasch. and C. marginiventris parasitized FAW larvae at rates of 82, 10, and 2% respectively. This high rate of parasitization by C. insularis in field cages and the field (Mitchell et al. 1984) indicated that C. insularis was the principal parasitoid of FAW in southern Florida.

Seventy, forty and thirty-nine percent of first instars were parasitized in treatments having 1, 2, and 3 paper sections respectively (Fig 12). Thirty percent of second instars were parasitized in 2 paper section treatment. These results were similar to those reported by Mitchell et al. (1984) where 77% of the first two instars were parasitized. Ashley et al. (1982) reported that the percent parasitization of the first 4 instars of FAW remined constant and then decreased substantially for 5th and 6th instars. Reasons for the reduction in percent parasitization in second instars was not properly understood. Mitchell et al. (1984) reported the decrease of

FIG. 12. Mean percent parasitized FAW instars in treatments 1, 2, and 3 paper sections inside field cage.


First instar
Second instar
Third instar
Fourth and fifth instar
PERCENT PARASITIZED FAW LARVAE
80
60
40
20
1
2
3
PAPER SECTIONS

the proportion of first instar larvae was probably a function of crop maturation as well as the larval population reaching a more stable age distribution. The greatest impact on FAW in all 3 treatments occured in first instars. This was similar to that reported by Vickery (1929) where first instars of FAW were preferred by C. marginiventris since they can be stung before dispersing from the egg mass. Thirty-five percent of third instars were parasitized in comparison to 15% of second instars in treatment 3.

The FAW larve that did not yield parasitoids produced FAW adults, starved to death because they did not feed on the diet or died from unknown causes. The proportion of nonparasitized larvae that yielded FAW adults was always greater than starved or died from unknown causes (Fig 13). Parasitoid sex ratios favored females in treatments having 3 egg masses per paper section (Table 14). Sex ratio regulation of C. marginiventris could be due to eigher selective fertilization of eggs or differential mortality of larvae depending on host density. Selective fertilization by C. marginiventis female in low host densities may be based on female detection of previously parasitized hosts. Many hymenopteran parasitoids can distinguish between parasitized and non-parasitized hosts (Wylie 1965) and fertilize a smaller percentage of eggs on parasitized hosts (Flanders 1939). If the female C. marginiventris

FIG. 13. Mean percent of FAW larvae that became a) adults, b) starved and died c) died from unknown reasons in treatments 1, 2, and 3 paper sections.

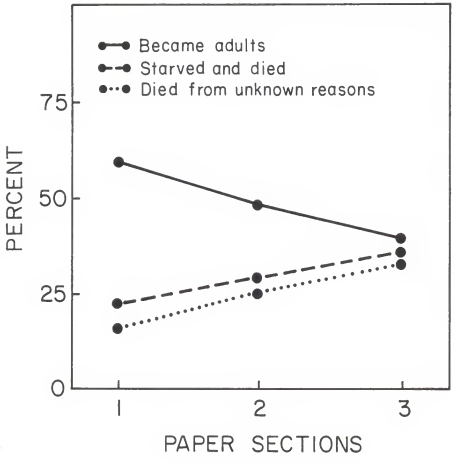

Became adults
Starved and died
Died from unknown reasons
75
50
25
0
PERCENT
1
2
3
PAPER SECTIONS

Table 14. Sex ratio ± SE (♀:♂) for *C. marginiventris* (C.m.) and *C. insularis* (C.i.) from FAW larvae parasitized inside a field cage.

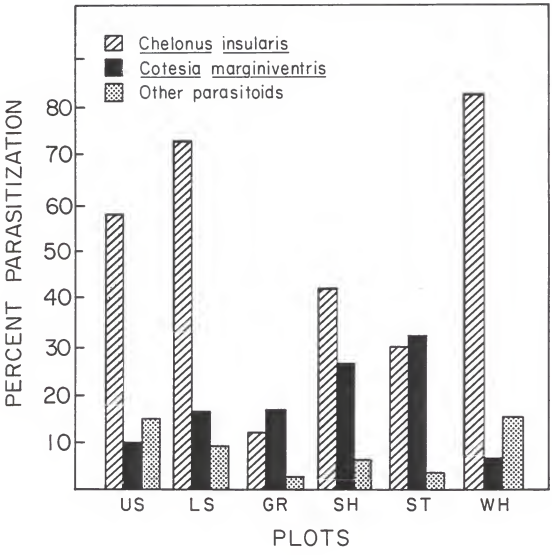
Egg mass size	C.m. Sex ratio (♀:♂)	C.i. Sex ratio (♀:♂)
<50 (1 Paper section)	1.00:5.5±0.9	1.90:1.00±1.6
>50 <120 (2 . .)	1.00:2.00±0.7	1.00:1.70±0.3
>120 <180 (3 . .)	3.5:1.00±1.3	2.9:1.00±0.9

was not capable of controlling fertilization of its eggs then high percent of males in low densities could be due to differential mortality resulting from competition among larvae for available food within the host. Local increases in the ratio of parasitoids to hosts can produce a change of sex ratio in field population of Hymenoptera (Charnov et al. 1977).

Experiment 3--Field Plots

C. insularis emerged as the predominant parasitoid (Fig 14) on the upper (58.5%), and lower (71%) leaf surfaces, between stalks and leaf sheaths (40.5%) and the control (80.5%). A higher percentage of C. marginiventris than C. insularis emerged from the treatments placed on ground (15.5%) and stalk (35.5%). Temelucha difficulis Dasch., Meteorus autographae Muesebeck Rogas laphygmae Viereck and several unidentified species accounted for the remaining parasitoids. Mitchell et al. (1984) and Ashley et al. (1982) reported that in order to abundance C. insularis. T. difficilis and C. marginiventris were the principal parasitoids collected from study plots at Homestead. Therefore, releasing C. marginiventris increased its parasitization level above that of T. difficilis. The percent parasitization was higher from the lower surface of leaves in comparison to the control. Morrill and Greene (1973) reported that in corn the highest number of FAW larvae were found in whorls.

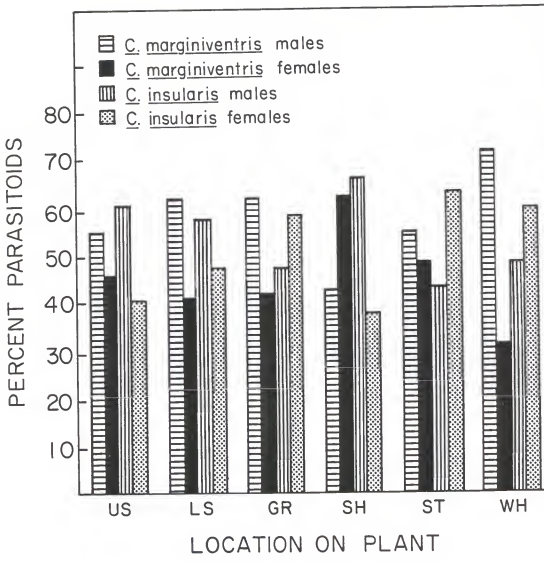
FIG. 14. Percentage parasitization for principal parasitisoid species recovered from FAW larvae from (US) upper surface of whorl, (LS) lower surface of whorl, (GR) ground, (SH) between stalks and leaf sheath, (ST) stalk and (WH) control in corn.


Chelonus insularis
Cotesia marginiventris
Other parasitoids
PERCENT PARASITIZATION
80
70
60
50
40
30
20
10
US
LS
GR
SH
ST
WH
PLOTS

Our results, indicated that eggs pinned to the lower surface of leaves in whorls had highest percent parasitization. This suggested that FAW parasitoids search plant regions where the highest number of FAW larvae are found. Since the whorl is the highest part of the plant, first or second stage larvae would move up into this area (Greene and Morrill 1970). This may have accounted for the low parasitization rates observed in hosts collected near the ground and on the stalk. Both, C. marginiventris and C. insularis were observed to be highly mobile and rapidly dispersed away from the release site. Therefore, releases could be made at several points in a field and the parasitoids would naturally disperse throughout the field. The preference of C. insularis for FAW eggs on the undersurface of corn leaves in early vegetative stages agreed with the findings of Waddill (1977) and Keller (1980) who reported this site as preferred location for oviposition by FAW females.

The sex ratio of emerging C. marginiventris favored males in hosts collected from the upper surfaces (55%) lower surfaces (60%) of the whorl, stalks (60%), near ground level (53%), and control (70%) (Fig 15). Larvae collected between stalks and leaf sheaths yielded more female parasitoids (61%). Males predominated in emergence of C. insularis in the treatments of upper surface, lower surface, and between stalks, and leaf sheaths.

FIG. 15. Sex ratio for C. marginiventris and C. insularis recovered from FAW larvae from (US) upper surface of whorl, (LS) lower surface of whorl, (GR) ground, (SH) between stalks and leaf sheath (ST) stalk and (WH) control in corn.


C. marginiventris males
C. marginiventris females
C. insularis males
C. insularis females
PERCENT PARASITOIDS
80
70
60
50
40
30
20
10
US
LS
GR
SH
ST
WH
LOCATION ON PLANT

Significantly more medium sized larvae (head capsule width = 0.8-1.2mm) were found between stalks and leaf sheaths and lower surfaces of the whorl (Table 15). Initially, there were more small than large larvae feeding under the lower surface and upper surface but this trend was gradually changed with more medium sized larvae found between stalks and leaf sheaths. The greatest difference between small and large larvae was found between upper leaf surface with small sized larvae. Ashley et al. (1980) reported that FAW larval abundance decreased on corn plant upper surface than lower surface and this reduced abundance may be indicative of preferred feeding locations. Our experiment showed that FAW larvae prefer feeding locations such as between stalks and leaf sheaths, and lower surface. Food quality, changes with feeding location and may alter or influence larval development in FAW (Keller 1980). Feeding inside the leaf sheaths and the lower surface of whorls may be a form of protection from natural enemies. Very few large larvae were recovered in all 5 treatments.

The damage to upper leaves in the whorl was significantly greater in nonparasitoid release plots than in parasitoid release plots (Table 16). These results suggest that differences in degree of damage between parasitoid release and non release plots were related to the impact of the parasitoids. Significant differences

Table 15. Mean percentage of small (0.2-0.7), medium (0.8-1.2), large (1.3-2.4) head capsule widths from FAW larvae collected from upper surface (US), lower surface (LS), ground (GR), between stalk and leaf sheath (SH) and stalk (ST) in corn. a/

Collection Date	Percent														
	Small					Medium					Large				
	US	LS	GR	SH	ST	US	LS	GR	SH	ST	US	LS	GR	SH	ST
May 14, 1983	15.6a	20.5a	2.0c	10.5b	0.5c	11.0b	15.0b	0.0c	15.0b	0.5c	0.0c	1.0c	0.0c	2.0c	0.0c
May 27, 1983	17.0a	10.5b	0.0c	15.0ab	0.0c	10.0b	17.0a	0.0c	12.0b	0.0c	3.0c	2.0c	0.0c	10.0b	0.0c
June 14, 1983	8.0b	10.5b	0.0c	25.5a	0.0c	8.0b	12.0b	0.0c	30.0a	0.0c	2.0c	1.0c	0.0c	3.0c	0.0c
June 28, 1983	10.0b	12.0b	0.0c	20.0a	0.0c	5.0c	10.0b	0.0d	21.0a	0.0d	5.0c	4.5cd	0.0d	12.0b	0.0d
Aug. 14, 1983	3.0cd	10.8b	0.0d	31.0a	0.0d	14.5b	3.0d	0.0d	14.0b	0.0d	5.0c	4.0cd	0.0d	12.0b	0.0d
Aug. 28, 1983	3.5c	12.5b	0.0d	29.0a	0.0d	3.0d	8.5cd	0.0d	19.0b	0.0d	6.0d	8.6cd	0.0d	0.0d	0.0d

a/ Means in the same row followed by same letter were not significantly different by Duncans Multiple Range Test (5% level).

Table 16. FAW damage to different regions of corn in plots where C. insularis (C.i.) and C. marginiventris (C.m.) were released.

Date of Observations	% Damage to Corn by FAW a/					
	C.m. and C.i. released			No parasitoids released		
	Upper Surface	Lower Surface	Stalk	Upper Surface	Lower Surface	Stalk
May 8	19.6b	12.9c	0.1d	30.5a	13.4c	0.0d
May 12	13.5b	9.7c	0.0d	43.6a	10.1c	0.0d
May 16	15.5a	5.7b	0.0c	15.7a	5.2b	0.0c
June 9	19.7b	30.3a	0.0c	18.9b	28.5a	0.0c
June 13	14.5a	13.5a	0.0b	16.7a	13.5a	0.0b
June 17	30.5b	9.5c	0.2d	53.5a	28.5b	0.0d
July 11	24.3a	14.7b	0.5c	22.5a	15.6b	0.3c
July 15	19.7a	19.5a	0.0b	19.3a	21.5a	0.0b
July 19	33.7a	19.6b	0.0c	34.5a	19.1b	0.0c

a/ Treatments in the same row followed by the same letter were not significantly different by Duncans Multiple Range Test.

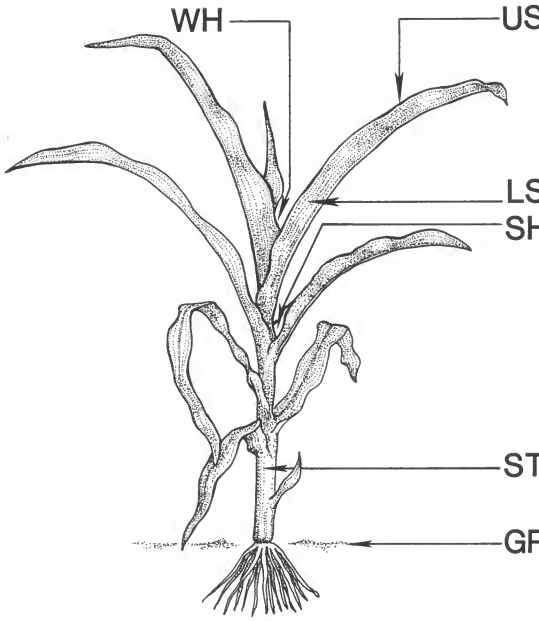
were observed on May 8th, 12th, and June 17th in terms of damage to upper leaves in parasitoid release and non release plots. Damage to lower leaves also showed significant differences between these two plots on June 17th. The damage to stalks were negligible in both plots. Keller (1980) reported that mature leaves are a qualitatively better food source for FAW than developing leaves. However, FAW larvae appar to prefer developing leaves under field conditions (Morrill and Greene 1973). Since feeding on mature leaves exposes FAW larvae to natural enemies and climatic changes, concealed feeding in whorls may have survival advantage. This trend was observed on all observatio dates except June 9, July 15, in non-parasitoid release plots and June 9th, in parasitoid released plots.

Cotesia marginiventris and C. insularis produced the most progeny at a host density of 64 eggs/larvae per cup. Longevity of C. marginiventris was greatest at a host density of 8 larvae/cup. Chelonus insularis had an emergence of 60% in field cages but C. marginiventris was a better competitor at host densities above 2 egg massses per paper section. Seventy percent of all hosts in the first instars were parasitized. Chelonus insularis emerged 72% and 58.5% of the time from parasitized larvae on the lower and upper surfaced of corn leaves, respectively.

Significantly more medium sized larvae were found between the stalk and the leaf sheath, on the lower surface of the whorl than in the other areas of the plant. The damage to upper leaves ws significantly greater in non-parasitized release plots than in parasitoid released plots.

FIG. 16. Illustration of exhibit the placement of egg containing paper sections in different regions of corn.

US Upper surface of whorl
LS Lower surface of whorl
GR Ground
SH Between stalk and leaf sheath
ST Stalk
WH Whorl region


WH
US
LS
SH
ST
GR

GENERAL SUMMARY AND DISCUSSION

Many factors influence the suitability of a potential insect host for parasitoid growth and development. For example, a host may be unsuited, if already parasitized or at stage of development inappropriate for parasitization. In the case of solitary parasitoids, prior parasitization of the host by another parasitoid of either the same or another species can result in a host not being suitable. Thus, if two solitary parasitoids occur in the same host, one individual usually destroys the other. Whether the competition involves physical attack, secretion of toxins, physiological suppression, or selective starvation, the outcome is largely dependent upon the species involved, the parasitization sequence, and the length of the interval between attacks. A myriad of parasitoids attack FAW (Ashley 1979) and their interrelationships influence the population dynamics of the pest. At present, the basic biological strategy control for FAW is to introduce as many suitable natural enemies as possible in the hope that the "best" species or combination of species will prevail. In this regard, available theoretical and empirical evidence indicated that the level of biological control usually increases as the number of natural enemy species increases (Huffaker et al. 1971). Results reported here

showed that interspecific competition occurred between exotic and indigenous FAW natural enemies. My data and that of Ashley et al. (1982) and Mitchell et al. (1984) indicated that is is difficult to establish additional natural enemy species in the overwintering range of FAW in South Florida, because of the dominance of C. insularis.

Host age preference, developmental period and longevity of M. manilae, a larval parasitoid of Spodoptera spp, imported from Thailand, were studied. First (24-48) and second (49-72 hrs) age group of FAW larvae found to be most suitable for parasitoid propagation. The developmental period ranged from 13-18 days. Male and female longevity was about 6-7 days. Parasitization rates of 3.5-30.1% by M. manilae in FAW larvae were observed. This biological information will be useful in the event that M. manilae is reared for inundative or inoculative releases in overwintering range of FAW.

Competition within FAW larvae by C. marginiventris, M. manilae and C. insularis revealed that C. marginiventris was a superior competitor compared to C. insularis but C. insularis was superior to M. manilae. Subsequent parasitization by either C. marginiventris or M. manilae of larvae exposed to C. insularis as eggs did not result in additive host mortality. Description and analysis of host finding behavior by C. marginiventris in FAW larvae previously parasitized by C. insularis showed

that this behavior consisted of 9 basic steps. These results supported the conclusion of Loke and Ashley (1984) that host finding behavior of C. marginiventris is influenced by chemicals from both plant and host. The percentage parasitization by C. marginiventris showed more than two fold increase in corn when compared to the increase in sorghum, Bermudagrass, and itch grass. M. manilae females significantly altered their behavior when hosts had already been parasitized by C. insularis.

C. insularis was the major parasitoid when FAW eggs were glued to upper surfaces of corn leaves (58.5%) lower surfaces (71%) and between stalks and leaf sheaths (40.5%). A higher percentage of C. marginiventris emerged from the treatments in the ground (15.5%) or the stalks (35.5%). Significant differences were observed with respect to damage to upper leaves in whorls of corn in parasitoid release plots than non parasitoid release plots and this was related to the impact of parasitoids on FAW larvae.

Additional work is needed in several areas and new avenues for research opened up as a result of information gathered from studies reported here. The superiority of one parasitoid over another in multiple parasitization results in the waste of some parasitoids. How this affects the comparative field efficiencies of all 3 parasitoids studied, as well as the population dynamics of

the FAW, should be investigated. The predominant native parasitoid, C. insularis, should be investigated to determine other characteristics important in controlling its impact on FAW larval populations. These include such characteristics as spacial distribution, temporal synchronization and reproductive rates. One of the major areas requiring further research is the mechanism of dominance in competition between parasitoids. I found evidence of physical attack by C. marginiventris on developing C. insularis larvae.

The potential impact of interspecific competition on FAW biological control needs further research and should include studies on: (1) competition studies between C. insularis and T. difficilis, since these two parasitoids are the principal species in the overwintering range of the FAW; (2) the effects of interspecific competition on parasitoid population densities; (3) more detailed studies on the developmental biologies of C. insularis, C. marginiventris and T. difficilis in FAW larvae; and (4) more detailed life table analyses of FAW larval populations. In addition, before more exotic parasitoids are introduced, it should be determined in controlled laboratory experiments if they can successfully compete within FAW larvae, with the native species.

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BIOGRAPHICAL SKETCH

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Rohan Rajapakse is a member of the Entomological Society of America, Florida Entomological Society and Sri Lanka Association of Advancement of Science. He has two sisters, Damayanthie (a high school teacher) and, Sandhya (an accountant).

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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